AMOM MENDES LUIZ

DIVERSITY, DISTRIBUTION AND CONSERVATION OF ANURANS FROM COASTAL PLAINS OF SÃO PAULO STATE, SOUTHEASTERN BRAZIL

DIVERSIDADE, DISTRIBUIÇÃO E CONSERVAÇÃO DE ANFÍBIOS ANUROS DAS PLANÍCIES COSTEIRAS DO ESTADO DE SÃO PAULO, SUDESTE DO BRASIL

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Dissertation presented to the Biology Institute of the University of Campinas in partial fulfillment of the requirements for the degree of Master, in the area of Ecology

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Orientador: RICARDO JANNINI SAWAYA

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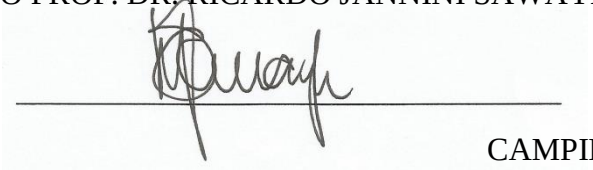

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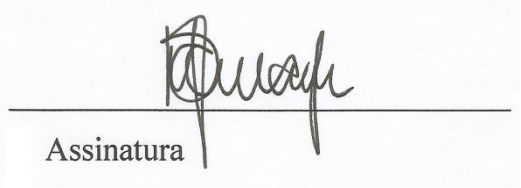

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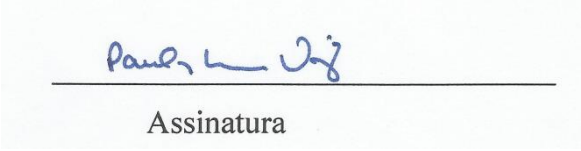

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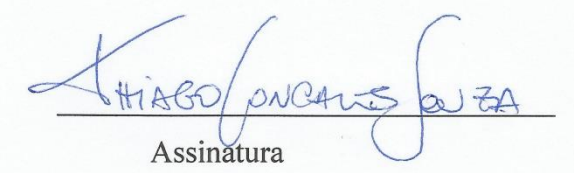

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ABSTRACT

Diversity, distribution and conservation of anurans from coastal plains of São Paulo state, Southeastern Brazil

Individuals and species are not randomly distributed in space. Hence, the communities composed by these species also show a spatial organization. Moreover, only few species can occur in many of the available environments. Therefore, the communities present a variation in their composition which can be spatially structured, that is, there are sites more similar each other in terms of species composition than other ones. Robert Whittaker named this phenomenon as the beta component of diversity or, simply, the beta diversity. The understanding of which processes generate and maintain beta diversity is a central question of the community ecology, also helping in the proposing and applying proper ways to its conservation and management. The aims of this study were to describe the anuran beta diversity patterns of coastal plains from southeastern Brazil and assess potential processes which influence such patterns. This study comprises two chapters. In the first one, I described aspects of the anuran beta diversity in the study region and evaluated how these patterns are protected in conservation units. In the second one, I seek to understand how multiple predictors could be related with the variation in species composition, given the theoretical and empirical framework on the influence of such predictors upon anuran diversity. The results of the first chapter showed a clear spatial pattern in the variation of species composition divided in three main areas that are congruent with the geomorphological history of the region. Still, we showed that the actual network of protected areas include similar beta diversity patterns to unprotected areas. However, the representativeness of these conservation units defined as the covered area (~ 4000 km²) is very small (11.3%). The results of the second

chapter demonstrated the relative importance of distinct predictors, including climate, geomorphological history and spatial scales, to explain the spatial variation of the anuran species composition. The beta diversity is mainly associated with spatial structure of geomorphological units. However, other processes are also important in structuring anuran communities, such as climatic gradients possibly related to the geomorphological structure and the presence of Serra do Mar range and broad scale processes. Our results have practical implications related to the choice of potential areas to coastal plains conservation in southeastern Brazil. In order to conserve the beta diversity patterns and their related processes, associated to unequal representativeness defined by the size area of protected areas, mainly on the central portions of São Paulo state coast, we suggested these areas as priorities in the planning and implementing of new conservation units.

RESUMO

Diversidade, distribuição e conservação de anfíbios anuros das planícies costeiras do estado de São Paulo, Sudeste do Brasil

Indivíduos e espécies não são distribuídos aleatoriamente no espaço. Consequentemente, as metacomunidades formadas por tais organismos também apresentam uma organização espacial. Associado a isso, poucas espécies conseguem se distribuir na maioria dos ambientes possíveis. Portanto, as metacomunidades possuem uma variação em sua composição que pode ser espacialmente organizada, ou seja, existem locais que são mais similares em termos de composição de espécies do que outros. Robert Whittaker nomeou esse fenômeno como o componente beta da diversidade, ou simplesmente, diversidade beta. Entender quais processos gera e mantém os padrões espaciais da diversidade beta é, portanto, uma questão central em ecologia de comunidades, além de auxiliar na proposição de formas apropriadas de manejo e conservação. O objetivo deste estudo foi descrever padrões de diversidade beta de anfíbios anuros das planícies costeiras do Sudeste do Brasil e investigar os possíveis processos que influenciam os padrões de diversidade detectados. A dissertação está dividida em dois capítulos. No primeiro capítulo, descrevo a diversidade beta de anuros da região de estudo e avalio como esses padrões estão protegidos atualmente, por unidades de conservação. No segundo capítulo, busco entender como múltiplos preditores poderiam estar relacionados com a variação na composição de espécies da região de estudo, dado o embasamento teórico e empírico da potencial influência de tais preditores sobre a diversidade de anuros. Os resultados do primeiro capítulo mostraram que existe um padrão claro de organização espacial na diversidade beta, estruturada em três áreas de forma congruente com a história geomorfológica da região. Os resultados

evidenciam ainda, que a atual rede de unidades de conservação inclui padrões de diversidade beta semelhante às áreas não protegidas. No entanto, a representatividade dessas unidades em termos de área (~ 4000 km²) é pequena (11.3%). Os resultados do segundo capítulo demonstram a importância de diferentes preditores, incluindo clima, história geomorfológica e processos espaciais em diferentes escalas, para explicar a variação espacial da composição de espécies de anuros. Dentre esses preditores, as unidades geomorfológicas foram predominantemente importantes para explicar a diversidade beta. No entanto, outros processos foram também importantes para a estruturação das comunidades, como por exemplo, o gradiente climático associado às unidades geomorfológicas, possivelmente gerados pela estrutura geomorfológica da região e pela presença da Serra do Mar e processos espaciais de ampla escala. Nossos resultados podem apresentar implicações práticas relacionadas à escolha de potenciais áreas para a conservação das planícies costeiras do Sudeste brasileiro. Tendo em vista a conservação dos padrões de diversidade beta e de seus processos subjacentes, associado à falta representatividade de em termos de tamanho de áreas protegidas na porção central do litoral paulista, sugerimos que tais áreas sejam priorizadas no planejamento e criação de novas unidades de conservação.

SUMÁRIO

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INTRODUÇÃO GERAL

Por que a presença e abundância de organismos variam de forma não aleatória no espaço? Ou seja, por que é que existe uma estrutura espacial na distribuição dos organismos? Obviamente, não há uma única resposta para essas perguntas, e nem mesmo uma que seja simples, embora uma organização conceitual seja possível (ver Vellend, 2010). Da mesma maneira, as comunidades ecológicas[1] formadas por tais organismos, não são agrupamentos aleatórios de espécies. Antes, tais comunidades geralmente apresentam variação em sua composição que não é espacialmente aleatória, ou seja, essa variação é espacialmente organizada (Dray et al., 2012). Portanto, descrever e investigar os padrões espaciais que emergem dessas comunidades é um alvo primário e desafiador para os estudos em ecologia de comunidades (Vellend, 2010). Além disso, a compreensão desses fenômenos é também de importância prática para o manejo adequado e a conservação da biodiversidade (Legendre et al., 2005), pois diferentes processos e seus padrões associados vão requerer diferentes estratégias de conservação para mantê-los.

Ao estudar a variação espacial na composição de árvores em relação a gradientes ambientais, Whittaker (1960) cunhou o termo diversidade beta para denominar essa variação espacial, ou seja, a mudança na composição de espécies entre comunidades. Desde a sua definição, uma miríade de métricas e significados para o termo diversidade beta têm surgido (ver revisão em Anderson et al., 2011; Tuomisto, 2010). Anderson et al. (2011) argumentaram a favor da pluralidade no conceito de diversidade beta, pois essa pluralidade seria útil no sentido de abranger a natureza complexa dos dados inerentes às comunidades ecológicas (mas veja Tuomisto, 2010). Assim, Anderson et al. (2011) dividem dois grandes grupos associados aos

[1] Aqui o termo comunidade ecológica é considerado de uma forma abrangente, a saber, um grupo de organismos com múltiplas espécies, que co-ocorrem em uma dimensão espaço-temporal específica (Vellend, 2010; mas veja Ricklefs, 2008).

conceitos de diversidade beta e suas respectivas métricas. O primeiro, denominado *turnover*, representa uma mudança direcional na composição da comunidade ao longo de um gradiente espacial, ambiental ou temporal pré-definido. O segundo corresponde à "variação" na composição entre unidades amostrais que não é direcional, ou seja, não se enquadra a nenhum gradiente explícito. A abordagem utilizada neste estudo se refere ao segundo grupo, devido à ausência de qualquer gradiente definido *a priori* para área de estudo.

O interesse dos ecólogos pelos estudos de padrões de diversidade beta aumentou expressivamente na última década (Anderson et al., 2011). Esse interesse especial se deve ao fato de que, a variação espacial na composição de espécies *per se*, representa um experimento natural, e por isso possibilita o teste de hipóteses específicas sobre determinados grupos de processos que geram e mantem a diversidade beta (Legendre et al., 2005; Legendre & De Cáceres, 2013). Dessa forma, podemos começar a responder perguntas semelhantes àquelas que fizemos anteriormente, como por exemplo, quais processos são responsáveis por gerar similaridade ou dissimilaridade na composição de espécies em diferentes comunidades?

Tradicionalmente, respostas à pergunta de quais processos possibilitam a co-ocorrência de espécies e consequentemente estruturam padrões espaciais de diversidade beta, estão profundamente arraigadas no conceito de nicho ecológico (Hutchinson, 1957; Ricklefs, 1987). A década de 60 foi extremamente importante para o desenvolvimento desse paradigma determinístico (Hutchinson 1957; MacArthur & Levins, 1967; Paine, 1966). A ideia central é que espécies ecologicamente similares, dentro de uma mesma comunidade, competem por recursos limitados, de tal forma que os nichos dessas espécies apresentam um limiar máximo de sobreposição. A partir desse limite, as espécies tendem a se excluir competitivamente e a espécie mais eficiente no uso do recurso prevalecerá (Hardin, 1960; MacArthur & Levins, 1967). Assim, dentro desse paradigma, interações locais entre as espécies são extremamente importantes para a

estruturação das comunidades, incluindo competição, predação, parasitismo e mutualismo (Paine, 1966; Bruno et al. 2003). Estudos sobre comunidades que investigam as relações entre espécies e o ambiente estão também baseados nesse paradigma, pois testam pressupostos de que haja uma forte relação do nicho ecológico da espécie com seu ambiente. Essa relação entre espécies e ambiente é um fator importante para estruturação de comunidades e é chamado de *controle ambiental* (Legendre et al., 2005; Legendre & Legendre, 2012).

É evidente que a diferenciação de nicho, relacionada ao ambiente, competidores, predadores e mutualistas, entre outros mecanismos determinísticos, é um importante fator na estruturação dos padrões de diversidade (Leibold & McPeek, 2006). Entretanto, a natureza contingente revelada por estudos empíricos de mecanismos relacionados ao nicho, e sua importância na estruturação das comunidades, revelou a necessidade de se reconsiderar outros processos e escalas de estudo (Lawton, 1999; Ricklefs, 1987; Ricklefs & Schluter, 1993).

Dessa forma, constatou-se que processos que ocorrem em escalas (*sensu* Levin, 1992) temporais e espaciais maiores do que a escala das comunidades locais também exercem uma influência direta sobre a composição das espécies (Ricklefs, 1987). Processos como especiação, extinção, dispersão, geomorfologia e a história biogeográfica da região foram reintroduzidos na interpretação dos padrões de diversidade encontrados na natureza (Ricklefs, 1987; 2006; 2008; Vellend, 2010). De fato, o estudo das comunidades a partir dessa perspectiva histórica e evolutiva ampliou o escopo de potenciais processos responsáveis por gerar e manter a biodiversidade, adicionando também elementos estocásticos, como por exemplo, extinções aleatórias (Vellend, 2010).

Se elementos estocásticos pudessem descrever a estrutura das comunidades tanto quanto elementos determinísticos relacionados ao nicho, quão universal seria a importância dos processos baseados em nicho? Essa questão motivou o desenvolvimento da Teoria Neutra da

Biodiversidade (Hubbell, 2001), enraizada nos conceitos da evolução molecular e biogeografia de ilhas (Rosindell et al., 2011). A partir dessa teoria, que inicialmente se opôs ao paradigma determinístico, os indivíduos são considerados como equivalentes ecológicos, ou seja, não haveria diferenciação de nicho. Parâmetros demográficos são completamente estocásticos, e esta característica predominaria na estruturação das comunidades. Mais recentemente, esse componente foi denominado de deriva ecológica (*ecological drift*; Hubbell, 2001; Vellend, 2010). Dessa forma, a variação espacial na composição de espécies é resultado exclusivamente da limitação na dispersão das espécies, que se dispersam aleatoriamente do *pool* regional e ainda, possivelmente, de novas espécies que evoluíram recentemente na metacomunidade[2] (Bell, 2005; Legendre et al., 2005; Tuomisto et al., 2012).

É difícil imaginar uma floresta tropical composta por centenas de espécies interagindo sem qualquer diferenciação de nicho, e sendo completamente estruturada por processos exclusivamente neutros, tais como deriva ecológica e dispersão estocástica (Leibold & McPeek, 2006, Rosindell et al., 2011). É claro que espécies devem ser diferentes de alguma forma, para que possamos considerá-las como espécies distintas (Leibold & McPeek, 2006). Entretanto, os atributos que conferem isolamento reprodutivo, pensando em espécies que se reproduzem sexuadamente, podem não ser ecologicamente relevantes. Por exemplo, proteínas de compatibilidade e reconhecimento gamético, que influenciam somente na fusão entre o espermatozoide e o óvulo, não possuem qualquer relevância ecológica imediata para a espécie. A existência de complexos de espécies crípticas, também evidencia a possibilidade da co-ocorrência de espécies que são ecologicamente muito similares. Assim, espécies ecologicamente equivalentes podem ter um importante impacto na estrutura das comunidades, o que pode ser

[2] Leibold et al. (2004) definem uma metacomunidade como um conjunto de comunidades locais que são ligadas por dispersão de múltiplas espécies potencialmente interativas.

congruente com processos neutros (veja Leibold & McPeek, 2006). Portanto, uma dicotomia entre as perspectivas neutra e baseada em nicho se torna de alguma forma artificial (Cottenie, 2005; Gravel et al., 2006; Leibold & McPeek, 2006). Assim, investigar os papéis relativos desses processos (históricos, neutros e de diferenciação de nicho) é de importância crucial para compreendermos melhor a variação espacial na composição das comunidades ecológicas, i.e., a diversidade beta.

Nesse contexto, o espaço tem sido considerado importante para explicar os padrões de variação espacial na estruturação das comunidades (Borcard et al., 1992; Dray et al., 2012; Griffith & Peres-Neto, 2006). Isso porque comunidades limitadas por dispersão apresentam autocorrelação espacial positiva, ou seja, aquelas mais próximas são mais similares entre si, em relação às mais distantes. Além disso, variáveis climáticas e geológicas, bem como outras variáveis ambientais (e.g., topografia), podem também apresentar estrutura espacial. Por fim, a interação interespecífica potencialmente possui uma estrutura espacial relevante, como é o caso de espécies territoriais (Dray et al., 2012).

Logo, considerar explicitamente a estrutura espacial em modelos que investigam a estrutura de comunidades se tornou essencial para a compreensão de processos que ocorrem em múltiplas escalas (Dray et al., 2012). Finalmente, o entendimento desses processos é também importante para a alocação apropriada de recursos e esforços para conservação da biodiversidade em diferentes escalas (Legendre et al., 2005; Noss, 1990), pois comunidades estruturadas por processos neutros necessitarão de estratégias de conservação distintas daquelas estruturadas processos históricos ou baseados em diferenciação de nicho (Legendre et al., 2005).

Sistema de estudo

Os anfíbios anuros são um interessante sistema para se descrever e investigar os padrões e processos descritos acima. Eles apresentam características fisiológicas peculiares, como pele permeável, ciclo de vida complexo (Wells, 2007), e são especialmente afetados por condições climáticas contemporâneas, como disponibilidade de água e variação de temperatura (Buckley & Jetz, 2007), assim como por fatores históricos, tais como história geológica e eventos de especiação (Valdujo et al., 2013). Anuros também podem ser caracterizados por apresentarem limitada habilidade de dispersão, embora, tal suposição não tenha sido testada de forma abrangente (veja Smith & Green, 2005). Além dessas caraterísticas ecológicas peculiares, a destruição e desconexão de habitats (Becker et al., 2007), além de doenças e alterações climáticas, tornam esse grupo extremamente ameaçado, alcançando uma das maiores proporções de espécies ameaçadas na região Neotropical (Loyola et al., 2013).

Objetivos

Os objetivos gerais desta dissertação são: (i) descrever os padrões de diversidade beta de anfíbios anuros das planícies costeiras do estado de São Paulo, Sudeste do Brasil; e (ii) avaliar possíveis processos relacionados a estes padrões. A dissertação está dividida em dois capítulos, em formato de artigos para publicação.

No primeiro capítulo descrevi o padrão de diversidade beta e discuti as possíveis implicações para a conservação da região de estudo. Para isso utilizei métricas usuais de diversidade beta e métodos multivariados de visualização e mapeamento do padrão encontrado. Além disso, avaliei a distribuição de Áreas Protegidas e comparei os padrões de diversidade beta dentro e fora dessas áreas. No segundo capítulo, investiguei as possíveis variáveis associadas ao padrão de variação espacial na composição de espécies, discutindo os potenciais processos

inferidos através de tais variáveis e relacionados ao padrão de diversidade beta. Utilizei métodos multivariados, análises de estrutura espacial em diferentes escalas, e a análise de partição da variação explicada por variáveis climáticas, espaciais e geomorfológicas. Há uma variedade de abordagens estatísticas para se analisar diversidade beta (veja discussão em Laliberté, 2008; Legendre et al., 2005; 2008; Pélissier et al., 2008; Tuomisto & Ruokolainen, 2008). Aqui utilizaremos a *"raw-data approach"* (Legendre et al., 2005), cuja diversidade beta é analisada diretamente da matriz de presença e ausência de espécies a partir de métodos multivariados (ver revisão em Dray et al., 2012). A partir dos resultados apresentados aqui, espero contribuir para a compreensão dos padrões de diversidade de anuros das planícies costeiras, assim como apontar os possíveis processos relacionados à distribuição da diversidade neste ambiente extremamente ameaçado.

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Capítulo 1

Anuran beta diversity patterns and conservation of Atlantic Forest lowlands in southeastern Brazil

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Abstract

Aims: To describe diversity patterns of anurans in Atlantic Forest's coastal plains. To assess the representativeness of protected areas in relation to beta diversity patterns in order to discuss implications to conservation for these highly threatened habitats.

Location: Restinga environments in coastal plains of the Atlantic Forest, southeastern Brazil.

Methods: We described anuran distributions in a 2,5 arc minutes grid cell system, based on field work, scientific collections, and literature data. We constructed a matrix of Sørensen pairwise dissimilarity to describe beta diversity patterns. We obtained the three first axes of PCoA from the dissimilarity matrix and converted them into a single RGB composite raster. Also, we performed a WPGMA cluster analysis in order to group cells based on pairwise dissimilarities and selected main clusters with a Mantel approach. Finally, we assessed protected area representativeness by calculating area covered by protected areas network of the study region, and by comparing beta diversity components (spatial turnover and nestedness) inside and outside of the protected areas network.

Results: We recorded 57 species belonging to 22 genera and 10 families. The mean richness by cell was 36 species. Five species (8.8%) were restricted to restinga environments. The RGB composite gradient clearly shows three distinct regions, north, central, and south. The WPGMA analysis resulted in three main clusters matching the RGB composite gradient. The beta diversity is more related to spatial species turnover than nestedness. Although, both protected and unprotected cells had similar overall patterns of beta diversity components, only 11.3% of the total area is covered by protected areas.

Main Conclusions: The beta diversity patterns of the coastal plains showed a structured spatial pattern which seemly correspond to natural geomorphological divisions of the region. This finding suggests that geomorphological history of the region can play an important role in the shaping the spatial structure of beta diversity patterns. Although beta diversity within protected areas showed the same overall pattern of unprotected ones, the representativeness described by the size of protected areas covering study region is low. Therefore, it is urgent to maintain and create new protected areas in areas without conservation units of the coastal plains studied here, in order to conserve effectively the biodiversity, specially the spatial species turnover which correspond to the main component generating the beta diversity of these threatened habitats.

Keywords: species turnover, nestedness, representativeness, geomorphological history, Serra do Mar, restingas, protected areas, biodiversity

Introduction

Describing patterns of species diversity in space and time is the first step towards the assessment of the potential processes underlying such patterns. Furthermore, biodiversity data are the basis for the indication and management of priority areas for conservation (Margules and Pressey, 2000). Among the patterns of species diversity detected in the nature, one of the most interesting is the variation of species composition across space (Legendre and De Cáceres 2013). Although community ecologists were more interested in spatial patterns of richness, the focus on the component of spatial variation in species composition has increased in the last decades (Melo et al. 2012). Whittaker (1960, 1972) termed the variation in the species composition among sites as the beta component of diversity or simply β diversity, and since this classical proposal of Whittaker, a myriad of measures to quantify beta diversity has been proposed and implemented (see review in Tuomisto 2010a, b).

The beta diversity of one region is related to two observable phenomena: nestedness and spatial turnover (Baselga 2010, but see Ulrich and Almeida-Neto 2012). These two different components emerge owing to antithetic processes. Nested species assemblages are produced by species loss or gain, which can be a result from a set of mechanisms, such as extinction and dispersal limitation (Ulrich et al. 2009), resulting in poorer species assemblages being subsets of richer ones (Baselga 2013). On the other hand, spatial turnover is the replacement of some species by others owing to environmental sorting, spatial and/or historical processes (Baselga 2010, Legendre et al. 2005). Recently, Baselga (2010, 2012) proposed a partition of the Sorensen

index to disentangle these two components of beta diversity patterns. Disentangling these two components can be important as a first step to infer the underlying processes which generate beta diversity patterns. Equally important, it is the discerning of these two components to the conservation planning, because spatial turnover and nestedness components will require distinct conservation strategies. For instance, if nestedness is predominant in a given region, richer areas should be prioritized, since poorer ones are subsets of these richer ones. But, if spatial turnover is the predominant component, conservation efforts should be directed to larger number of different sites within of the region, and not exclusively to the richer ones, in order to properly preserve the patterns and their related processes (Baselga 2010).

Furthermore, the most commonly used approaches to systematic planning is based on beta diversity patterns, such as complementarity, however, few methods use explicitly beta diversity metrics (McKnight et al. 2007, but see Nóbrega and De Marco Jr. 2011). The use of estimates of compositional changes spatially explicit could provide benefits to conservation efforts, because ultimately, it is the rate of species composition changing along space that drives the optimal spatial arrangement of protected areas (McKnight et al. 2007). Moreover, using the beta diversity metrics in the selection of new protected areas would help to take account particular ecological and historical processes that the simple species counts could not express (McKnight et al. 2007). In this sense, mapping beta diversity and recognizing areas with particular composition has been considered an additional and important tool to improve conservation planning (Devictor et al. 2010, McKnight et al. 2007), especially in Neotropical region which shows higher congruence of variation in the species composition among different vertebrate groups, and high rates of beta diversity (McKnight et al. 2007, Melo et al. 2009).

The Neotropical Atlantic Forest harbors one of the highest degrees of species diversity, endemism and threat of the entire planet (Myers et al. 2000, Ribeiro et al. 2009). Despite its importance, the causes of its overwhelming diversity are not completely clear, particularly the causes of its high beta diversity. Some studies pointed out that beta diversity is high owing to high environmental heterogeneity (Pardini and Umetsu 2006) and historical factors (Pardini 2004, Rocha et al. 2008). Although these processes underlying beta diversity patterns are not completely clear, understanding how these patterns are currently conserved by the network of protected areas is essential to policy decisions.

Among different landscape units of the Atlantic Forest, the Brazilian coastal plains or the restingas have been intensively occupied, deforested, and fragmented since its colonization (Rocha et al. 2007). Large natural areas were lost early in the Brazilian colonization, with the remaining areas restricted to isolated fragments and still under constant pressure from urban development, mineral extraction, infrastructure development, among other threats along the most densely populated portions of Brazil (Silva et al. 2012, Rocha et al. 2007, Ribeiro et al. 2009).

The term "restinga" describes the quaternary sediments deposited during oceanic incursions (Suguio and Tessler 1984). In the broadest sense, this term can be applied to a complex of vegetal physiognomic forms (i.e., fields, scrubs, and forests) established during the quaternary deposition of sediments along the Brazilian coast (Cerqueira 2000, but see Marques et al. 2011). Owing to its peculiar vegetation adapted to considerable stress levels (such as soil nutrient deficiency, low soil organic matter content, and high salinity), restinga habitats are relatively fragile environments, imposing additional challenges for habitat restoration (Rocha et al. 2005). Additionally, the floristic and historical uniqueness of restinga indicate that

conservation plans should consider all coastal lowland vegetation as a priority in the conservation planning of the Atlantic Forest (Marques et al. 2011).

The knowledge of anuran species of the restinga environments is still incipient and basic data on anuran diversity is sparse. Carvalho-e-Silva et al. (2000) listed 52 amphibian species and concluded that endemism in such habitats is low (i.e., five species). Rocha et al. (2008) conducted a large anuran inventory in several restinga habitats along the Brazilian coast, founding five species previously unrecorded in the restinga habitat. However, they did not surveyed most of the southern portions of the Atlantic Forest. Carvalho-e-Silva et al. (2000) included southernmost areas, but they did not perform systematic fieldwork or included large scientific collection databases. Thus, we thought that the low richness previously observed for restinga is owing to undersampling. In the face of intense changes in this environments caused by human occupation, the knowledge of basic data about restinga diversity patterns is the first step to understand the underlying ecological processes and making decisions for conservation planning of this fragile and extremely threatened habitat.

Herein, our aims are twofold. We first describe the anuran diversity of restinga forest areas of São Paulo state, Southeastern Brazil, based on field sampling and extensive revision of vouchers in scientific collections. We then evaluate the conservation status of the region through of extension covered by the network of protected areas in the region and compare beta diversity components for protected and unprotected areas.

Material and Methods

Study Area

The study area encompasses most of the coastal region of São Paulo and southern Rio de Janeiro states, defined by Suguio and Martin (1978). This region is naturally bounded due to its particular geomorphological history, with about 550 km of extension. The coastal plains of this region are bounded on southern and northern by Precambrian basements of the Serra do Mar complex (Suguio and Martin 1978). Internally, this region shows two large divisions, hereafter, northern and southern units. The northern unit is characterized by the presence of Precambrian basement reaching the sea, creating relatively small coastal plains and rugged coastlines. The south unit has larger coastal plains due the differential uplift of the Precambrian basement (Suguio and Martin 1978). The coastal plains within this region are separated by narrow headlands of Precambrian rocks (Suguio and Martin 1978). The vegetation is composed usually by restinga forests and ombrophilous lowland forests (Marques et al. 2011). Bromeliads (Bromeliaceae) are a typical vegetational group of these environments and play an important role in the establishment of other plant species. Additionally, the water tank of bromeliads provides resources to invertebrate and vertebrate species, including shelter and reproductive sites for anurans.

Field Work

We carried fieldwork in four sites, within both southern and northern units, at Ubatuba, Bertioga/São Sebastião, Itanhaém and Iguape municipalities. We sampled adult anurans species by means of searching reproductive sites (Heyer et al. 1994) and complete species inventory (Heyer et al. 1994) adapted by Rocha et al. (2004). For searching in reproductive sites, we selected five water bodies including temporary and permanent ponds in each site. For the complete species inventories, we selected five transects within restinga forests, at least 500 meters apart from each other in each locality. Species were sampled by bioacoustics records and

through active and careful searching in all suitable microhabitats for frogs along each transect and ponds (Rocha et al. 2004). Each pond and transect was sampled three times from October 2011 to May 2012. This sampling design was adopted in order to maximize the likelihood to find frogs during the breeding season of most Atlantic Forest species (Bertoluci 1998, Bertoluci and Rodrigues 2002) and in the available sites.

Sampling in scientific collections

We examined 9,730 specimens belonging to 57 species which were recorded in the study area and deposited in the scientific collections: Célio F. B. Haddad (CFBH), from Universidade Estadual Paulista, Campus Rio Claro, and the Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso" (ZUEC). We also gathered species occurrences from literature (see Appendix S1) and compared species richness with other studies of restinga environments in Brazil (e.g., Bastazini et al. 2007; Carvalho-e-Silva et al. 2000; Vilela et al. 2011). We excluded rheophilic species (genera *Cycloramphus*, *Crossodactylus*, *Hylodes*, and *Thoropa*) because such forms are associated with rocky streams in foothill and mountain environments, which are the boundaries of the restingas in the study region and typically associated with Ombrophilous forests.

Species occurrence data

We described the geographic distribution of each species by means of α-hulls, which are a generalization of minimum convex polygons (see Burgman and Fox 2003) based on records collected on the field and scientific collections, using *alphahull* R package (Pateiro-López and Rodríguez-Casal 2011). This method calculates the average length of all lines which connect the species records through a Delaunay triangulation, and after exclude lines longer than this average

length, avoiding biases of the minimum polygon convex method related to the shape and species habitat (Burgman and Fox 2003). The polygons of species distributions were processed to record specie's presence/absence in a 2,5 arc minutes (*ca.* 5 km²) grid cell system on the study area, up to 100 meters above sea level (Figure 1), using R package *raster* (Hijmans 2013). In the Brazil, protected areas are classified according to their conservation aims, defined as sustainable use areas and integral protection areas. Integral protection areas are free from human interference and planned exclusively to conservation and research of biodiversity, while sustainable use areas associate sustainable exploration of natural resources with conservation of the biodiversity. We used the official map of protected areas of Brazil (PAs, http://mapas.mma.gov.br/ i3geo/datadownload.htm) to overlay the PAs polygons onto our grid cell and considered the cells inside of these polygons as protected cells. Then, we constructed three matrices: a matrix of species by sites (**Y**), a matrix of species by protected cells ($\mathbf{Y_P}$), and a third matrix of species by unprotected cells ($\mathbf{Y_U}$). Final dataset (**Y**) included 368 cells, with only 40 representing protected cells ($\mathbf{Y_P}$).

We classified species distribution as follows: (i) restricted: any species with distribution restricted only to restinga environments; (ii) typical: species that have their distribution highly associated with restinga environments, but found occasionally in non-restinga habitats within Atlantic Forest; (iii) widespread: generalist species that occurs in restinga environments as well as in other Atlantic Forest (Ombrophilous forests and Semidecidual forests) and Cerrado habitats.

Data Analysis

To describe and visualize the beta diversity on the study region, we used multivariate ordination and cluster analysis. Cluster analysis search to discontinuities in resemblance between

samples (e.g., beta diversity), which could be obscured in a reduced dimensionality from the ordination methods. However, given the continuous nature of most ecological communities along space, ordination methods are mandatory in order to describing multivariate structure from communities (Legendre and Legendre 2012). Therefore, ordination methods and cluster analysis can be used complementarily, when one aims to describe both, discrete unities and continuous variation of structures in the ecological community's data (Legendre and Legendre 2012).

So, we firstly, calculated the pairwise Sørensen's dissimilarity index (β_{sor}) to visualize the overall beta diversity patterns on the map (Figure 1), producing a square matrix (**S**) of dissimilarity among sites (i.e., cells). We then performed a Principal Coordinates Analysis (PCoA), which preserves original distances between objects in the multidimensional space of the ordination (Legendre and Legendre 2012) using R package *vegan* (Oksanen et al. 2011). After, we selected the first three axes, so that each cell had a score based on ordination performed by PCoA. These three axes with cell scores were converted to raster surfaces and combined as a single RGB composite raster, so that axes represent one of colors of the RGB raster (see Rosauer et al 2014). Furthermore, similar colors in the map represent low compositional dissimilarity between cells (low Sørensen index between cells), and different ones represent high compositional dissimilarity between cells (high Sørensen index between cells), using ArcGis 10.1 (ESRI, 2012).

To identify cell groups which reflect the potential breaks in species turnover, we used the pairwise β_{sor} distance matrix in a cluster analysis, WPGMA (Weighted Pair-Group Method with Averaging), using hclust function from *stats* R package. WPGMA is a hierarchical agglomerative clustering which calculates the arithmetic average distances between clusters, weighting the contribution of clusters when grouping new cells in the clustering process. In this way, each cell

contributes equally to the clustering. To identify an appropriate number of clusters, we used an approach based on Mantel correlation between distance matrices. This method correlates the original distance matrix (i.e., β_{sor} matrix) with several binary matrices where each one represents different levels of grouping and then, chooses the level (i.e., binary matrix) which had the highest correlation (*r*) with original distance matrix (see Borcard et al. 2012).

We enumerated the PAs present in the study region (Table 1) and assessed their representativeness by calculating the area of coastal plains covered by PAs of the study region, using ArcGis 10.1 (ESRI, 2012). Additionally, to assess if PAs have different patterns of beta diversity components (i.e., nestedness and spatial turnover) compared to the unprotected areas, we tested if the means of nestedness and spatial turnover values from protected ($\mathbf{Y_P}$) and unprotected areas ($\mathbf{Y_U}$) are significantly different. For this, we used two-sample permutation tests with *perm* function of the *perm* R package (Fay and Shaw 2010), at 0.05 significance level.

The beta diversity components of $\mathbf{Y_P}$ and $\mathbf{Y_U}$ were calculated using the metrics proposed in Baselga (2010). These metrics represent additive partitions of beta diversity measured through Sørensen index for multiple sites (β_{SOR}; Baselga et al. 2007), which is an overall metric which describes both spatial turnover and nestedness. Spatial turnover is measured by Simpson dissimilarity index for multiple-sites (β_{SIM}; Baselga et al. 2007), and the nestedness component (β_{NES}; Baselga 2012) is the difference between β_{SOR} and β_{SIM}. It is important to note that β_{NES} is not a metric of nestedness *per se*, instead it is a fraction of total dissimilarity which is not caused by species replacement, but by richness differences (Baselga 2012). We calculated nestedness and spatial turnover components with *beta.sample* function of *betapart* R package (Baselga and Orme 2012), using 20 sample cells selected randomly 1000 times. This function resamples sites (i.e., cells in the grid) randomly and recalculates beta diversity components each time, in order to

obtain mean and standard deviation values, which were used to compare nestedness and spatial turnover values of $\mathbf{Y_U}$ and $\mathbf{Y_P}$ with permutation tests quoted above. Since $\mathbf{Y_U}$ matrix has disproportionally more cells in the southern unit, this could bias the calculation of beta diversity components (Baselga 2012). To avoid this problem we sampled randomly 30 southern cells to compare beta diversity in protected and unprotected cells.

Results

We recorded 57 species, belonging to 22 genera and 10 families (see Appendix S1). The mean richness *per* cell was 36 species (range: 29 to 44; SD = 4). We classified five species as restricted (*Aparasphenodon bokermanni*, *Scinax littoralis*, *Physalaemus atlanticus*, *Arcovomer passarellii*, and *Chiasmocleis carvalhoi*) and five species as typical (*Aparasphenodon brunoi*, *Aplastodiscus eugenioi*, *Dendropsophus decipiens*, *Scinax argyreornatus*, and *Physalaemus spiniger*) of restinga environments (Appendix S1).

Anuran beta diversity varied from 0 to 0.39 between cells. The spatial pattern of compositional dissimilarity represented by the three first PCoA axes corresponded to 96.7% of variation in the species composition matrix. The first axis described 63%, the second described 29.3%, and the third described 4.41% (see Appendix S2 with scores of each axis mapped). The RGB composite gradient (Figure 1a) showed the species dissimilarity throughout the study region, which seems to correspond at least to three distinct regions, namely: northern, central and southern. Mantel correlation (r) between binary matrices (n=15) representing different set of clusters and β_{sor} distance matrix, ranged from 0.02 to 0.73. The best set of clusters (r = 0.73) contained three main groups (Figure 1b), which separated cells from northern, central and southern portions of the study region.

Protected areas covers only 11.3% of the study region and are distributed irregularly along three distinct regions showed by RGB composite gradient (Table 1, Figure 2). Both protected and unprotected cells had similar overall patterns for beta diversity components, with spatial turnover (β_{SIM}) greater than nestedness. The spatial turnover of protected (β_{SIM}=0.42, SD=0.05) and unprotected cells (β_{SIM}=0.41, SD=0.04) were not significantly different (P = 0.11). However, nestedness component of protected (β_{NES}= 0.13, SD=0.01) and unprotected (β_{NES}= 0.14, SD=0.02) were different (P<0.05). The difference in the nestedness component probably occurs owing to unprotected cells have 57 species, whereas the protected cells included 55 species, since this metric is directly affected by species richness. Therefore, it has not an ecological meaning, and might represent a statistical artefact.

Discussion

Species diversity

Recent large-scale studies on anuran diversity in restinga environments have concluded that both endemism and richness are low, with about five and 52 species, respectively (Carvalho-e-Silva et al., 2000; Rocha et al. 2008). We recorded a low number of species restricted to restinga environments, corroborating this pattern of low endemism for anuran and other vertebrate groups in the restinga (Cerqueira 2000). The speciation of vertebrate endemics in these environments seems to be related to the isolation of populations by sea level oscillations during the Pleistocene and Holocene (Cerqueira 2000; Mantovani 2003). It is possible that the low endemism and richness of these environments would be owing to time-for-speciation effect (Kozak and Wiens 2010), which states that intermediate elevations have more species because these elevations were occupied longest and had more time for speciation and accumulation of

species, when compared with highest and lowest adjacent elevations. But this hypothesis remains to be tested, for instance, in altitudinal gradients of Atlantic Forest. Since coastal plains were recently colonized after holocenic marine regressions, it would be necessary to understand the earlier speciation patterns in the higher sites of Serra do Mar and posterior colonization by clades in highest and lowest extremes in the altitudinal gradient.

Although the literature on anuran diversity in restinga is still sparse, the simple comparisons of our data and recent studies (Bastazini et al. 2007; Carvalho-e-Silva et al. 2000; Narvaes et al. 2009; Telles et al. 2012; Vilela et al. 2011; Wachlevski and Rocha 2010; Zina et al. 2012) show that the restinga studied here is one of the richest througout Brazilian coastal plains. It is reasonable to assume that the Serra do Mar species pool is an important element influencing this higher richness. Owing its peculiar physiological characteristics, such as permeable skin and water dependence for reproduction in most species (Wells 2007), amphibian richness has been associated with contemporary environmental drivers of diversity, particularly water and temperature (Buckley and Jetz 2007, Silva et al. 2011, Vasconcelos et al. 2010). The Serra do Mar mountain chain in this region retains the wet air masses from Atlantic Ocean, causing orographic rains (Marques et al. 2011). Hence, the region has one of the highest rainfall indices of the Brazilian coast (Gutjahr and Tavares 2009) and consequently it is suitable to harbor a rich fauna of anurans. Additionally, given that older adjacent areas than restinga habitats are pools of species which can colonize them (Cerqueira 2000, Marques et al. 2011), the richer fauna of Serra do Mar (Haddad 1998) could be considered as an important pool of colonizers in the past, after holocenic marine regressions.

Beta diversity patterns

The visualization of beta diversity patterns of the study region and the groups evidenced from clustering analysis, clearly shows important breaks in the species composition, which seems to correspond in some extension with subunit breaks of Precambrian rocks proposed by Suguio and Martin (1978). This spatial correspondence between geomorphological units and species dissimilarity occurs mainly in the northern and southern subunits; however the central portion seems to be a single unit considering species composition. Rocha et al. (2008) pointed out that historical and biogeographical processes can play an important role in structuring anuran assemblages throughout the restingas (Rocha et al. 2008). Historical processes, such as age and formation of coastal plains, and biogeographical processes, such as *in situ* speciation, extinction and immigration are fundamental to generate current patterns of diversity in the restingas (Cerqueira 2000). Thus, for understanding of processes underlying the beta diversity patterns of the restingas studied here, we should consider explicitly its particular geomorphological history, which can represent relevant historical processes quoted above.

Moreover, it is well known that beta diversity is generated and maintained by multifaceted processes which occur in multiple scales (Anderson et al. 2011, Cottenie 2005, Dray et al. 2012, Legendre et al. 2005, Tuomisto et al. 2008). Contemporary climate and other environmental variables (e.g., topography) which potentially determine species distribution, as well as, spatial processes based on neutral theory, are important drivers of community structure (Cottenie 2005, Leibold and McPeek 2006). These two processes are not mutually exclusive. Instead, they can represent endpoints of a continuum in the shaping of structures in the biological communities (Leibold and McPeek 2006). The Serra do Mar differential uplift generated coastal plains with different size areas, and supposedly, with differences in the climate. Towards to the south, coastal plains are larger because Serra do Mar is more distant from the sea. Since, coastal plains nearest

of the range slope are wetter than farther ones, towards to the south, the climate can become less wet and consequently can be an important driver of the community structure. Therefore, understanding to what degree each processes contribute to spatial variation in the species composition is an important step towards the knowledge of underlying processes structuring anuran assemblages in restingas studied, and consequently, to management decisions (Legendre et al. 2005).

Conservation implications

Beta diversity components (i.e., nestedness and spatial turnover) of protected and unprotected cells were similar, which suggests that protected areas represent well the beta diversity of whole study region. Meanwhile, only 11.3% of the whole study region is protected by conservation units, that is, the representativeness in terms of size area covered by protected areas is very small. Since we consider the whole area, regardless the areas actually forested and suitable to conservation (i.e., forested fragments), the representativeness of protected areas may be even smaller. It could be evidenced considering the fact that, only 4% of the original restingas and associated habitats (e.g., mangroves) still remains in the Serra do Mar region, as showed by Ribeiro et al. (2009). The restingas environments have been severely explored in the last centuries, since the Brazilian colonization. These areas were preferentially occupied and currently have one of the highest demographic densities of Latin America. Hence, its biodiversity is critically threatened (Rocha et al. 2005). Our results have important implications to conservation planning of restinga environments in southeastern Brazil. Spatial species turnover seems to be predominant in the study region, as evidenced by high spatial turnover component values of protected and unprotected cells. It implies that, even poorer areas can have a distinct composition

and particular species. Thus, such poorer areas must also be considered in the conservation planning, in order to conserve the beta diversity patterns of the studied coastal plains.

The simple visualization of protected areas distribution in these coastal plains shows the lack of conservation units in the central and southernmost portions (Figure 2). Although Serra do Mar State Park covers virtually all surrounding of the coastal plains studied here, it protects predominantly areas around 100 meters above sea level, that is, most coastal plains of this region is out of Serra do Mar State Park boundaries. For instance, the municipalities in the central and southern portions (e.g., Itanhaém, Mongaguá, Peruíbe, Santos, and São Vicente) have the highest demographic densities (SMA, 2006) and virtually have not conservation units which protect restinga habitats. Therefore, based on our results, we consider these portions as priority to implementing of new PAs, in order to conservation of suitable forested areas that still remain in this portion, the conservation of biodiversity patterns and the underlying processes which generate and maintain them.

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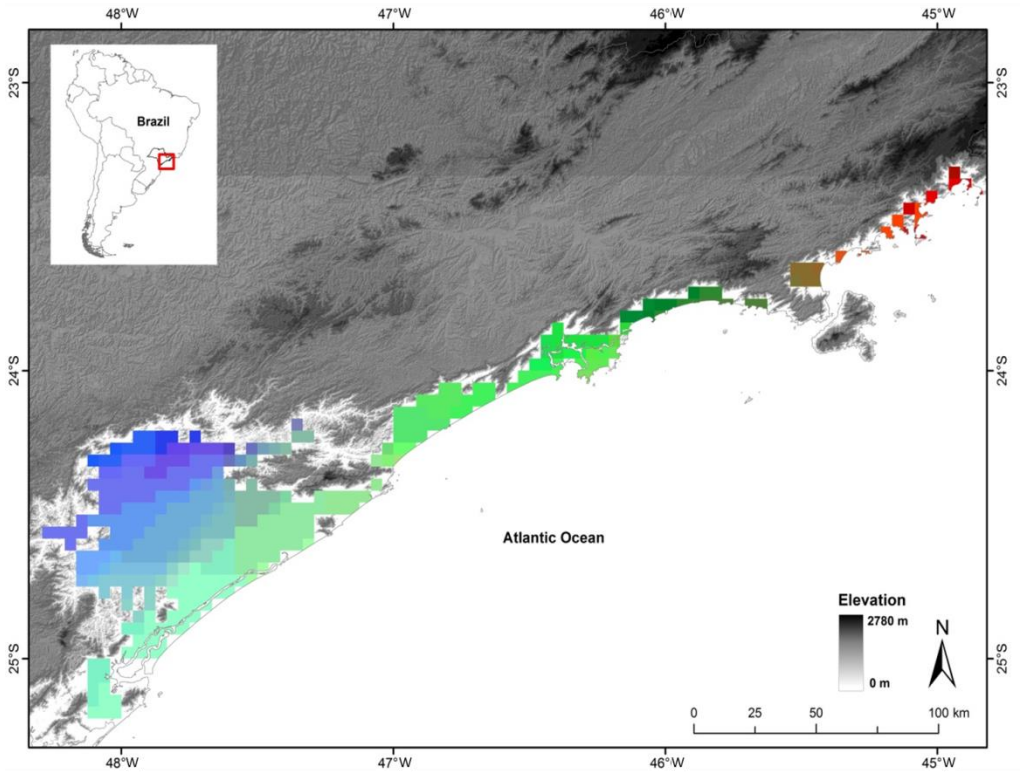
Table 1 Representativeness of protected areas in the study region considering total area (km²), the area which covers the studied region (%) and beta diversity components for protected areas network.

Name	Total Area (km^2)	Covered Area (%)	B_{SOR} / β_{SIM} / β_{NES}
Estação Ecológica Juréia - Itatins	792.4	6.0	
Parque Estadual Campina do Encantado	23.6	0.6	
Estação Ecológica Chauás	26.9	0.6	
Parque Estadual Ilha do Cardoso	225	0.6	
Parque Estadual da Serra do Mar	3153.9	2.3	
Parque Estadual das Restingas de Bertioga	93.1	1.3	
Total	4314.9	11.3	0.55 / 0.42 / 0.13

(a)


48°W
47°W
46°W
45°W
23°S
24°S
25°S
Brazil
Atlantic Ocean
Elevation
2780 m
0 m
N
0
25
50
100 km

(b)

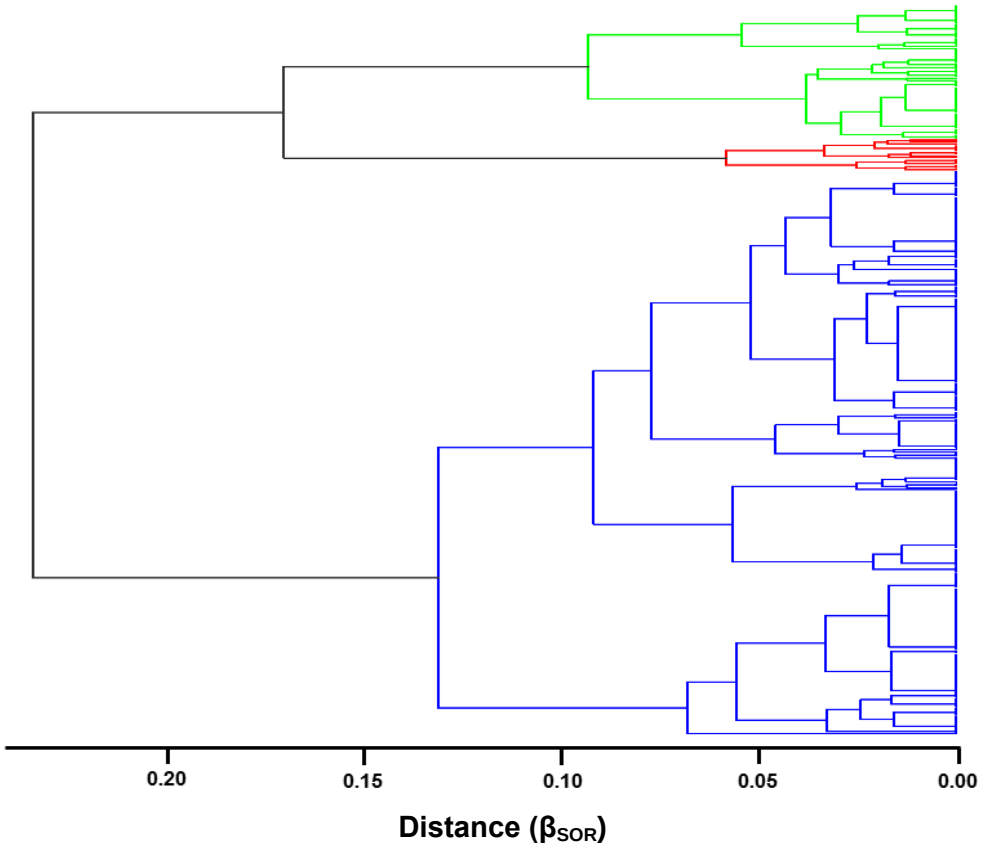

0.20
0.15
0.10
0.05
0.00
Distance (βSOR)

Figure 1 (a) Map of the study region showing beta diversity patterns expressed by PCoA axes of Sørensen pairwise dissimilarity matrix. The first axis represented by blue colors in the RGB composite map, described 63% of variation in the species composition matrix, the second one (i.e., green colors in the RGB composite map) represented 29.3%, and the third axis (i.e., red colors in the RGB composite map) described 4.4% (see Appendix S3). Similar colors between cells in the map represent low compositional dissimilarity (low Sørensen index between cells) and different ones represent high compositional dissimilarity (high Sørensen index between cells). (b) Dendrogram of the WPGMA analysis showing the three groups defined through Mantel correlation. Tips of the dendrogram represent cells of the grid. Red group represent cells of the north, green group represent cells of the central portion, and blue group represent cells of the south.

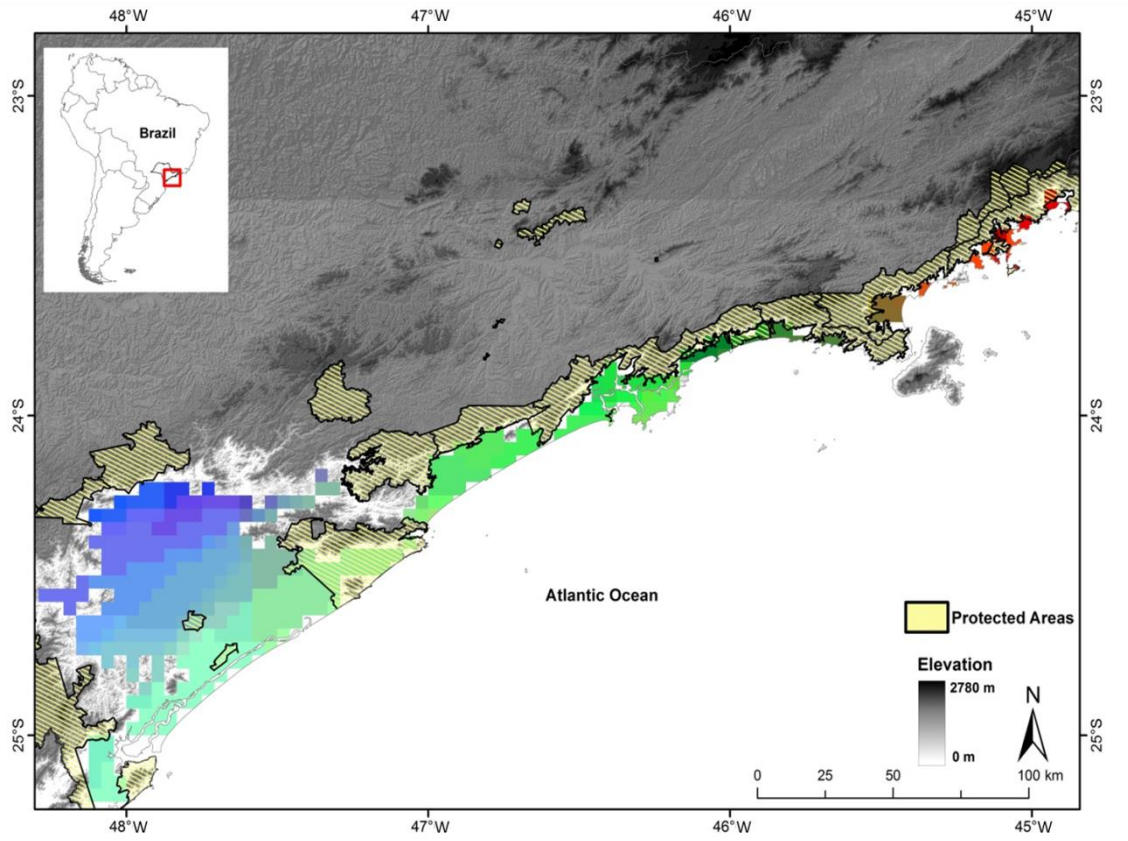


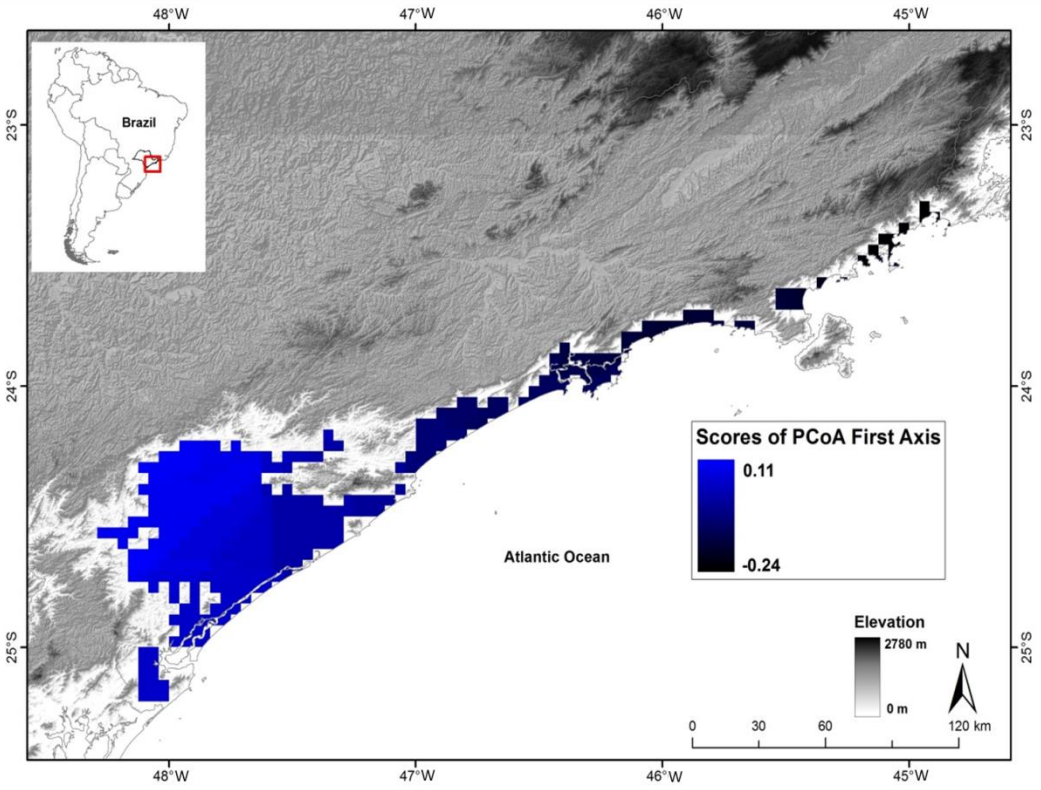
Figure 2 Map of the study region showing beta diversity patterns and polygons of protected areas. Protected cells are those covered by polygons of protected areas.

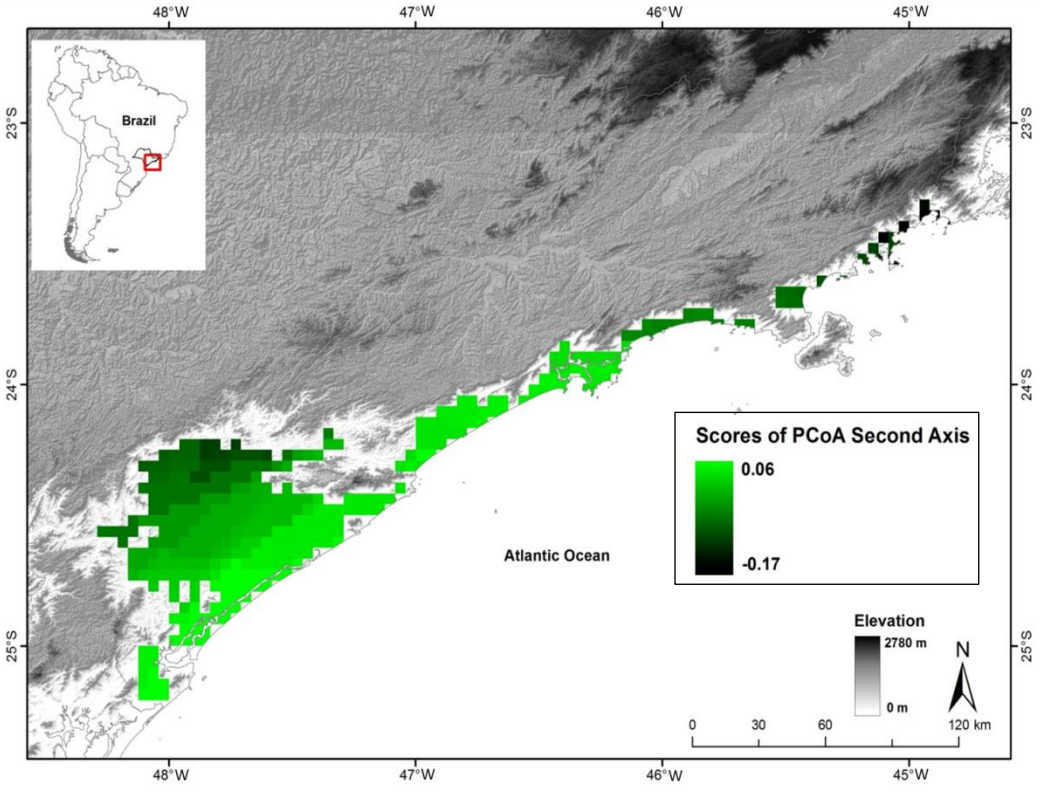
Appendix S1 Anuran species recorded in the restinga forests from coastal plains of São Paulo state, classified as restricted, typical or widespread (see Material and Methods) and its main source . FW: field work performed in present study; RC: records from scientific collections; RL: records from literature (see Appendix S1).

Species	Restricted	Typical	Widespread	Source
Brachycephalidae				
Brachycephalus hermogenesi			X	RC; RL
Ischnocnema bolbodactyla			X	RC; RL
Ischnocnema guentheri			X	RC; RL
Ischnocnema parva			X	FW; RC; RL
Bufonidae				
Dendrophryniscus brevipollicatus			X	FW; RC; RL
Dendrophryniscus leucomystax			X	FW; RC; RL
Rhinella hoogmoedi			X	FW; RC; RL
Rhinella icterica			X	FW; RC; RL
Rhinella ornata			X	FW; RC; RL
Ceratophryidae				
Ceratophrys aurita			X	RC; RL
Craugastoridae				
Haddadus binotatus			X	FW; RC
Hemiphractidae				
Fritziana fissilis			X	FW; RC
Fritziana ohausi			X	RC
Hylidae				
Aplastodiscus arildae			X	RL; RC
Aplastodiscus eugenioi		X		FW
Aparasphenodon bokermanni	X			FW; RC; RL

Aparasphenodon brunoi		X		RC; RL
Dendropsophus berthalutzae			X	FW; RC; RL
Dendropsophus decipiens		X		FW; RC
Dendropsophus elegans			X	FW; RC
Dendropsophus giesleri			X	FW; RC; RL
Dendropsophus microps			X	FW; RC; RL
Dendropsophus minutus			X	FW; RC; RL
Dendropsophus werneri			X	FW; RC
Hypsiboas albomarginatus			X	FW; RC; RL
Hypsiboas faber			X	FW; RC; RL
Hypsiboas raniceps			X	RC; RL
Hypsiboas semilineatus			X	FW; RC; RL
Itapotihyla langsdorffii			X	FW; RC; RL
Phyllomedusa distincta			X	FW; RC; RL
Phyllomedusa rohdei			X	RC; RL
Scinax angrensis			X	RC; RL
Scinax argyreornatus		X		FW; RC
Scinax catharinae			X	FW; RL
Scinax eurydice			X	FW; RC
Scinax hayii			X	FW; RC
Scinax imbegue			X	FW; RL
Scinax littoralis	X			FW; RC
Scinax perpusillus			X	FW; RC; RL
Scinax perereca			X	RC; RL
Scinax tymbamirim			X	FW; RL
Scinax trapicheiroi			X	FW; RC; RL

Trachycephalus mesophaeus			X	FW; RC; RL
Leiuperidae				
Physalaemus atlanticus	X			FW; RC; RL
Physalaemus bokermanni			X	FW; RC; RL
Physalemus moreirae			X	RC; RL
Physalaemus spiniger		X		FW; RC; RL
Leptodactylus latrans			X	FW; RC; RL
Leptodactylus marmoratus			X	FW; RC; RL
Myersiella microps			X	FW; RC; RL
Elachistocleis cesarii			X	RC; RL
Chiasmocleis leucosticta			X	FW; RC; RL
Chisasmocleis carvalhoi	X			FW; RC; RL
Arcovomer passarellii	X			FW; RC; RL
Odontophrynidae				
Macrogenioglottus alipioi			X	RC; RL
Proceratophys appendiculata			X	FW; RC; RL
Proceratophrys melanopogon			X	FW; RC; RL
Total	5	5	47	


48°W
47°W
46°W
45°W
23°S
24°S
25°S
Brazil
Atlantic Ocean
Scores of PCoA First Axis
0.11
-0.24
Elevation
2780 m
0 m
N
0
30
60
120 km


48°W
47°W
46°W
45°W
23°S
24°S
25°S
Brazil
Atlantic Ocean
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0 m
N
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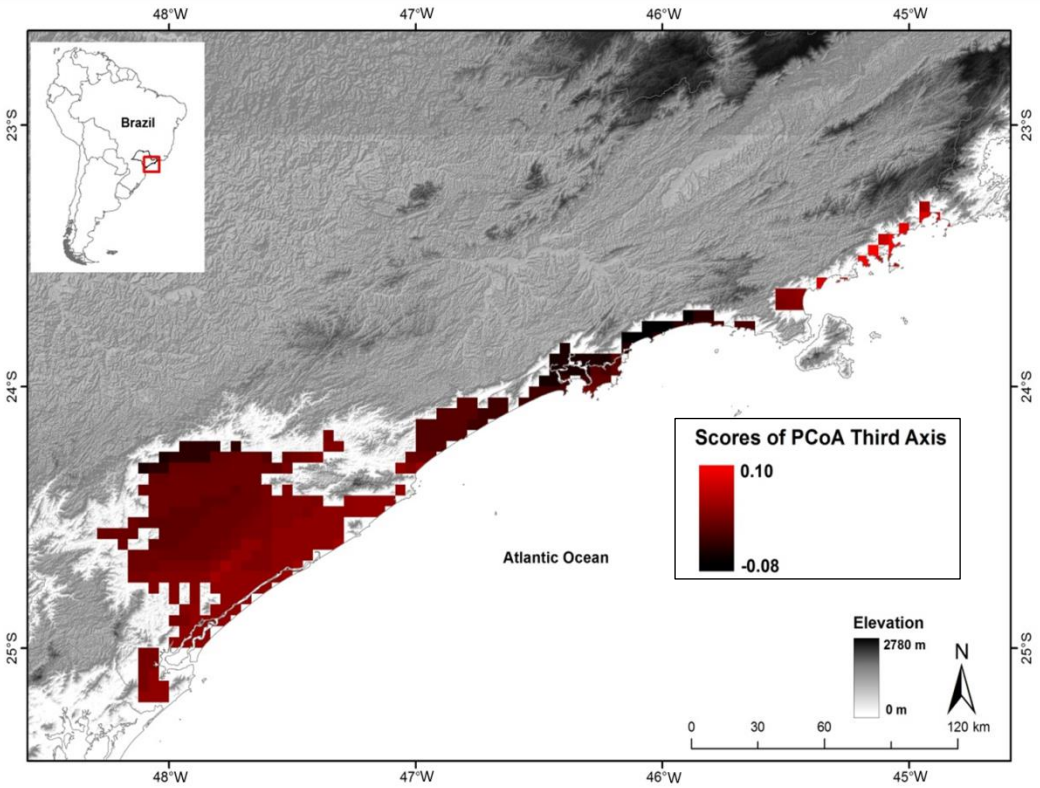
120 km



Appendix S2 Maps of PCoA ordination scores of the first three axes which described 96.7% of the spatial variation of anuran species composition (i.e., beta diversity), based on pairwise Sørensen's dissimilarity index. Each axis represent one color which composed the RGB composite raster (Figure 1). The first axis described 63% of variation in the species composition, the second one represented 29.3%, and the third one described 4.4%.

Capítulo 2

Assessing geomorphological, climatic and spatial drivers to anuran beta diversity from Atlantic Forest lowlands

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Abstract

Beta diversity is the result of multiple processes, such as niche-based, neutral, and historical processes, which occurs in several scales. Owing to peculiar biology and limited dispersal ability, anuran assemblages can be affected by contemporary climate, as well as, by dispersal-based processes. Herein we assess the climatic, spatial, and geomorphological correlates of anuran beta diversity from coastal lowlands of the Atlantic Forest in southeastern Brazil. Anuran composition was described based on fieldwork, specimens deposited in scientific collections, and literature records. Partial redundancy analysis was performed to partition the explained variation of anuran composition by geomorphological, climatic, and spatial predictors. The beta diversity is spatially structured in larger scales. Geomorphological variables were the most important predictor (36%) to describe beta diversity in the region. Shared fraction between climate and geomorphological history was the second most important fraction (16%). Explained variance by broad scales after controlling effects for the remaining predictors was the third most important fraction (11%). Our results suggest that historical factors related to geomorphology of the region played a crucial role in structuring the anuran beta diversity. The complex relationship between geomorphological history and climatic gradient generated by the Serra do Mar Precambrian basement seems to be another important factor to spatial structure of beta diversity. These results highlighted the importance of consider explicitly variables that represent historical processes, jointly with contemporary variables, in order to evidence the synergic effects of distinct sets of predictors to beta diversity, as such effects are inherent from the complex nature of ecological communities.

Keywords: niche-based processes, dispersal-based processes, historical factors, anuran assemblages, Eigenfunction analysis, spatial variables, variation partitioning, biogeography

Introduction

Spatial organization of diversity patterns is one of the most interesting properties of ecological communities (Legendre and De Cáceres 2013). The last two decades have witnessed a growing focus on the study of spatial patterns of variation in species composition (Anderson et al. 2011, Melo et al. 2012). The variation in species composition among sites was termed by Whittaker's seminal works (1960, 1972) as the beta diversity component of species diversity. The particular interest in beta diversity can be attributable to the fact that the study of variation in the species identity along space, allow us to infer more directly what set of processes drives the structure of the biodiversity, while the simple species counts (i.e., alpha diversity) are not able to express such explicit variation in the species composition (Tuomisto and Ruokolainen 2006, Legendre et al. 2005, Burgess et al. 2010). Moreover, such studies provide the so-called "mensurative experiments", since broad-scale manipulative experiments are not feasible (Hurlbert 1984, Legendre & De Cáceres 2012).

Considering the multifaceted and multiscale nature of ecological communities, any dichotomized perspective (e.g., regional versus local diversity; see Gonçalves-Souza et al. 2013) of the processes structuring them, would be oversimplistic (Gravel et al. 2006, Leibold and McPeek 2006, Burgess et al. 2010). However, such paradigmatic divisions can be in fact useful, as a start point to move on towards to integrative frameworks, about the relative importance of the several processes which structure ecological communities (e.g., Leibold et al. 2004, Logue et al. 2010, Winegardner et al. 2012). Between these distinct processes, niche differentiation among co-occurring species has been traditionally invoked as a primary processes structuring ecological communities, which are deeply rooted on niche theory (Hutchinson 1957, MacArthur and Levins 1967, Vellend 2010). There are several important factors influencing the diversity patterns under

the “umbrella” of niche-based processes, such as the use of limited resources, predation, parasitism, competition, as well as environmental conditions which the species are adapted (Vellend 2010). One of the predictions of beta diversity patterns regarding niche-based processes is that, species distributions and community structure are closely related with environmental variables which in turn are ecologically relevant to species niche (Legendre et al. 2005, Tuomisto and Ruokolainen 2006), termed as environmental control (Legendre and Legendre 2012).

However, processes occurring in greater spatio-temporal scales can also play important roles in structuring communities (Ricklefs 1987, 2008). Processes that occur in regional scales, such as speciation and dispersal of immigrants from the regional species pool, can be balanced with negative effects of competitive exclusion and unfavorable environmental conditions in local communities (Ricklefs 1987, Ricklefs and Schluter 1993). Geological history for instance, can generate barriers and corridors which might create spatial patterns in specific species distributions and, consequently, in the community structure (Ricklefs 1987). In fact, this historical perspective reveals how some stochastic elements may be relevant to the diversity patterns, such as speciation through genetic drift (Ricklefs 2008, Vellend 2010).

In this sense, neutral theory makes clear assumptions about preeminence of random processes in structuring communities (see Hubbell 2001, Rosindell et al. 2011). The neutral theory assumes that individuals are ecologically equivalents, and it means that demographic parameters are completely stochastic (i.e., ecological drift). Although species need to be different in some way to we can recognize them as different species, the assumption of ecological equivalence is reasonable and does not imply that species are equivalent in all aspects of its phenotype and ecology (Leibold and McPeek 2006). For instance, species can differ in traits which promote reproductive isolation, but not have necessarily ecological relevance, as we can

see in complexes of cryptic species co-occurring, evidencing that neutral processes could be an important component of community dynamics (Leibold and McPeek 2006). Consequently, the variation in species composition would be the result of stochastic but spatially restricted dispersion (Tuomisto and Ruokolainen 2006), rather than niche differentiation among species. This neutral dynamic would generates clear positive spatial autocorrelation structures in the ecological communities (Diniz-Filho et al. 2012).

Thus, in fact, the challenge is understand the relative contributions of several processes occurring in distinct spatial scales, and their interactions to the structuring of ecological communities. Accordingly, the use of different sets of variables, such as climatic and geological variables, which able us to infer processes related to these predictors, has been one popular and useful approach in community ecology (Borcard et al. 1992, Legendre and Legendre 2012). Spatial variables *per se* has been regarded as an important surrogate to identify some of these potential multiscale processes underlying to variation in the species composition, rather than a nuisance aspect of spatial dependence in the statistical modelling (Legendre 1993, Griffith and Peres-Neto 2006, Dray et al. 2006, 2012). Therefore, to incorporate explicitly the space in the models it would help to the understanding and disentangle of the relative roles of niche, historical, and neutral processes in community ecology (Legendre 1993, Dray et al. 2012).

Owing to their peculiar traits, such as permeable skin, and complex life-history, anuran species distributions are known to be affected by abiotic factors, particularly, temperature, precipitation, and humidity levels (Keller et al. 2009, Buckley and Jetz 2007, Silva et al. 2012, Valdujo et al. 2013). These environmental conditions directly affect the physiological performance and geographic range limits of anuran species (Wells 2007). Furthermore, it is assumed that the dispersal abilities of anurans are limited (but see Smith and Green 2005). It

suggest that both, constraints to dispersal, such as geological barriers, and neutral dynamics under restricted dispersal as explained above, could be equally relevant as drivers to the spatial patterns of anuran beta diversity. Herein we aim to assess the climatic, spatial and geomorphological correlates of anuran beta diversity patterns from the threatened coastal lowlands of Atlantic Forest, southeastern Brazil. Although multiple processes can influence patterns of beta diversity, based on influence of abiotic factors in the anurans distribution and limited dispersal of the group, we expect that the predictor's relative contributions will be greater to climatic and geomorphological variables.

Material and Methods

Study Area

The study area encompasses most of the coastal region of São Paulo and southern Rio de Janeiro states, with about 550 km of extension. Its geomorphological history was described and defined by Suguio and Martin (1978): the coastal plains of this region are bounded on southern and northern portions by Precambrian basements (i.e., Serra do Mar). Internally, it shows two large divisions, the north and south regions. The north is characterized by the presence of Precambrian basement reaching the sea, creating relatively small coastal plains. On the other hand, the south has larger coastal plains due the differential uplift of the Precambrian basement.

Furthermore, the coastal plains within this region are naturally separated by narrow headlands of Precambrian rocks which divide the region in four geomorphological subdivisions (Figure 1, Suguio and Martin 1978). It is worthy to note that these Precambrian natural divisions are older than coastal plains which ecological communities have established after marine regressions in the Quaternary period (Suguio and Martin 1978).These four geomorphological

units were used here as categorical predictors of species composition in the multivariate analysis (see below). The vegetation of this region is composed usually by restinga forests and Ombrophilous lowland forests (see Marques et al. 2011). Besides, Bromeliads (Bromeliaceae) are a typical component of these environments and play an important role to the establishment of other vegetal groups, beyond to providing resources to invertebrate and vertebrate species, as shelter and reproductive sites for anurans.

Species occurrence data

We carried out fieldwork in four sites within the four subdivisions proposed by Suguio and Martin (1978), at Ubatuba, Bertioga/São Sebastião, Itanhahém, and Iguape municipalities (Figure 1). We sampled adult anurans species through "search in reproductive sites" (Heyer et al. 1994) and "complete species inventory" (Heyer et al. 1994) adapted by Rocha et al. (2004). We selected five water bodies for "search in reproductive sites", including temporary and permanent ponds in each site, totaling 20 sampled ponds in the study region. We selected five transects within forests for the "complete species inventory", at least 500 m apart from each other in each locality, totaling 20 sampled transects. Species were sampled by bioacoustic records and through active searching on all suitable microhabitats for frogs along each transect and ponds (Rocha et al. 2004). Each pond and transect was sampled three times from October 2011 to May 2012. This sampling design was adopted in order to maximize the likelihood of finding frogs during most of the breeding season in all sites.

We examined 9,730 specimens of the 57 species which had known records in the study area and had been deposited in the following scientific collections: Célio F. B. Haddad (CFBH), from Universidade Estadual Paulista, Campus Rio Claro, and the Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso" (ZUEC). We excluded rheophilic

species (genera *Cycloramphus*, *Crossodactylus*, *Hylodes*, and *Thoropa*) because such forms are associated with rocky streams in foothill and mountain environments, which are the boundaries of the restingas in the study region and typically associated with Ombrophilous forests.

Finally, based on records collected in the field and scientific collections, we described the geographic distribution of each species by means of α-hulls, using *alphahull* R package (Pateiro-López and Rodríguez-Casal 2011). This method calculates the average length of all lines which connect the species records through a Delaunay triangulation, and excludes lines longer than this average length, avoiding biases of the minimum polygon convex method related to the shape and species habitat (Burgman and Fox 2003). The polygons of species distributions were produced in order to record specie's presence in a 2,5 arc minutes grid cell system (*ca.* 5 km²) on the study area, up to 100 m above sea level (Figure 1), using functions from R package *raster* (Hijmans 2013). The southernmost subdivision has disproportionally more cells than other geomorphological units (see Figure 1). We then randomly sampled 60 cells of this unit, and the final data set (**Y**) included 164 rows of sites and 57 columns of species. **Y** was Hellinger transformed (Legendre and Gallagher 2001).

Climatic and geomorphological variables

Climatic descriptors were compiled from the 19 bioclimatic variables of the WorldClim database (Hijmans et al. 2005), at the resolution of 2,5 arc minutes (~ 5km²), and we extracted values of climatic variables from each cell in our grid, generating a matrix of rows representing sites and 19 columns representing climatic variables. We excluded variables highly correlated (Pearson's r > 85%) and those which we not have a plausible interpretation about their influence on anuran ecology, such as isothermality. Based on these criteria, only four variables were

selected: temperature seasonality, mean temperature of the coldest month, precipitation seasonality and precipitation of the driest quarter. We then performed a Principal Component Analysis (PCA) in order to avoid multicollinearity among remained climatic variables, which artificially increase explained variation, and consequently causing type I error (Graham, 2003). The three axes with PCA scores were used as an explanatory matrix (**Clim**) in the subsequent multivariate analysis. These three first PCA axes accounted respectively, 67.4%, 24.4%, and 4.34% of the variation in the climatic variables of the study region. Table 1 summarizes correlation between climatic variables and PCA axes.

We used the four geomorphological units defined by Suguio and Martin (1978) as a categorical predictor of the species composition, so that each cell of the grid pertains to one of the four units: Cananéia/Iguape, Itanhaém/Santos, Bertioga/São Sebastião, or Ubatuba units (Figure 1). The categorical variables (**Geo**) were coded as dummy variables (Borcard et al. 2011). Additionally, it is important to note that these geomorphological units are spatially explicit, however they have a different ecological meaning from the component purely spatial assessed here. These units can represent historical processes (e.g., biogeographical processes) which may influence beta diversity in the region, thus, it is useful consider them explicitly in the beta diversity analysis of the study region.

Data analysis

To remove spatial linear trends (e.g., latitudinal trends) found in our data, which prevent us to model more detailed spatial structures, we detrended species composition matrix (Borcard et al. 2011, Legendre and Legendre 2012). Subsequently, to describe spatial structure of our data and generates spatial predictors to explain variation in the species composition, we used spatial

eigenfunction analysis (Griffith and Peres-Neto 2006; Legendre and Legendre 2012) based on Moran Eigenvector Maps (MEMs, see Dray et al. 2006, Peres-Neto and Legendre 2010). This method consists of eigenvector decomposition of connectivity matrices, namely the MEMs. The eigenvalues of these MEMs represent Moran's I statistic and then can describe spatial autocorrelation in different spatial scales (see details in Dray et al. 2006).

A crucial step in the MEM approach is the definition of a neighborhood matrix, which describes spatial relationship between objects (Dray et al. 2006). In our case, it is necessary to define which sites (i.e., cells) are neighbors and which are not. Then, to define neighborhood relationship between sites, we used a heuristic approach in which we tested several neighborhood distances, beginning by distance obtained through minimum spanning tree algorithm (Borcard and Legendre 2002) up to a maximum distance between sites. The best distance to construct the neighborhood matrix were selected based on corrected Akaike information criteria using *test.W* function of the *spacemakeR* R package (Dray 2013; R scripts to these procedures can be found in Borcard et al. 2011). MEMs with positive eigenvalues were generated from the best neighborhood matrix, and the best set of MEMs was selected through forward selection with double criteria based on adjusted R^2 statistics (Blanchet et al. 2008). Positive eigenvalues from MEMs represent positive spatial autocorrelation, because they are linearly correlated with Moran's I index (see Dray et al. 2006).

Additionally, to describe spatial variation of the species composition in distinct scales, we divided the MEMs in submodels, according to scales which they represent. It is possible owing to the orthogonal property of MEMs and multiscale spatial structure which they are able to model. The submodels and their associated scales can be defined according to (i) the study aims, (ii) by the similarity in the periodicity of spatial structure of significant MEMs (Ali et al. 2010,

Legendre et al. 2012), and (iii) by visual inspection of eigenvectors in the map (Laliberté et al. 2009). We defined two submodels which represented broad (**Broad**) and fine (**Fine**) scales which were used as spatial predictors in the multivariate analysis (see examples in Figure S1). Ecologically, these two scales can represent processes spatially structured in distinct scales, such as climatic conditions, dispersal and interspecific competition. Lastly, considering the spatial nature of geomorphological variables, it would be expected to find correlation between MEMs and geomorphological units. Therefore, to avoid collinearity in the model, we removed MEMs which were correlated with geomorphological variables (Pearson's $r > 0.3$).

We used redundancy analysis (RDA) and partial RDA to partition the explained variance in species composition, attributable to different set of explanatory variables: climatic, geomorphological, broad, and fine scale predictors (Borcard et al. 1992, Peres-Neto and Legendre 2010). The explained variation was expressed by unbiased adjusted R^2 statistics (R^2_{adj}, Peres-Neto et al. 2006). We used a hierarchical approach to partition the explained variance, which assumes a downscale priority of processes structuring the species composition, such as geomorphological history and broad scale climatic variables (see Legendre et al. 2012). Total variance explained by climate, geomorphological units, broad and fine scales were decomposed in 14 fractions corresponding to individual and shared fractions of the predictors. RDA was preferred because previous detrended correspondence analysis reveals a "short" gradient in the response matrix (i.e., **Y** Hellinger transformed) (Legendre and Legendre 2012). All these procedures were performed using functions of *vegan* and *ade4* R packages (Dray et al. 2013b, Oksanen et al. 2013). Furthermore, the significance of independent fractions was tested by permutation using *anova.cca* function of the *vegan* package (Oksanen et al. 2013).

Results

Fifty neighborhood matrices were tested with different maximum distances to the nearest cell, varying from 22.36 (i.e., distance obtained by minimum spanning tree algorithm) to 380 km, which is the maximum distance between cells in our grid. Model selection based on corrected Akaike information criteria (AICc) of distinct neighborhood matrices had AICc values ranging from -50.19 to 167.15. The best neighborhood matrix model (AICc= -50.19) has a maximum distance to nearest neighbor of 22.36 km. Forward selection in the MEMs with positive eigenvalues, selected a set of spatial variables with 21 MEMs. Then, we grouped MEMs in broad and fine scales, based on visual inspecting of them in the map and in the similarity in the periodicity (Figure S1). Eleven MEMs were classified as broad scale and 11 as fine scale (Figure S1). However, we had to exclude five broad scale MEMs (i.e., MEMs 2,3,4,6, and 10), because they showed correlation values with geomorphological units greater than r>0.3 (see *Data Analysis*), which could lead to misinterpretation of spatial structure of the beta diversity.

All individual fractions (i.e., climatic, geomorphological, broad, and fine) were significant, at alpha level of 0.05. The whole model with climatic, geomorphological, broad and fine scales variables described 74% (R^2_{adj}=0.74) of the beta diversity in the study region (Figure 2). Variation explained purely by climatic predictors was 3% (fractions [a] R^2_{adj}=0.03, Figure 2). The fraction shared by geomorphological and climatic variables described 16% of the variation in the beta diversity. Geomorphological history was the most important fraction to explain beta diversity, describing 36% of variation in the species composition (fraction [b], R^2_{adj}=0.36, Figure 2). Spatial variables classified as broad scales were the third most important fraction which significantly accounted 11% of the beta diversity (fraction [c], R^2_{adj}=0.11). Lastly, spatial

variables grouped in fine scales described 7% of the anuran beta diversity in the studied region (fraction [d], R^2_{adj}=0.07, Figure 2).

Figure 3 shows the site scores of the two first RDA axes mapped in the studied coastal plains. These two axes represent the ordination of the anuran beta diversity constrained by all predictors (i.e., geomorphological, climatic, broad, and fine scale variables), and accounted 58% of the variation in the anuran composition of the studied region. Then, they show how beta diversity is spatially structured in relation to all predictors, mainly by the geomorphological variables, which were the most important predictor to the variation in the anuran composition of the coastal plains.

Discussion

We found a clear spatial structure of the beta diversity pattern of the coastal plains, southeastern, Brazil. Moreover, considering the spatial context of our study area, we found that spatial pattern of beta diversity is structured mostly in larger scales. It can be evidenced by visualizing of the map scores of the first two RDA axes (Figure 3), and consequently by the two predictors that explained the most part of variation in the species composition (Figure 2), specifically, the geomorphological history which itself is a spatial predictor of larger scales, and the MEMs classified as broad scale. The reasoning behind this finding is that ecological systems could be affected by processes which follow a downscale spatial hierarchy (Wu and David 2002). Based on this theory, we can expect that the processes which occur in broad scales, such as geomorphological processes could generate broad-scale signatures in the structure of ecological communities (Legendre et al. 2012), as our results evidenced here.

Contrary to our expectations, the fraction explained uniquely by climatic variables was low (3%). However, the fraction shared by climate and geomorphological history explained 16%. Shared fractions between climatic or other environmental variables, and spatially explicit variables, such as geomorphological units or MEMs, are difficult to interpret because can represent ambiguous sources of variation (Peres-Neto and Legendre 2010). There are some possibilities to the source of variation in these shared fractions: (i) if this fraction represent spatial correlation in the community composition owing to the measured climatic factors, which in turn are spatially structured, then this fraction can be interpreted as spatial structure induced by climate; or (ii) if there are relevant missing predictors which are spatially structured and such predictors covariate with the measured climatic variables, then this fraction could not be interpreted unambiguously (see Peres-Neto and Legendre 2010).

Regarding our study region, there would be a third possibility to the interpretation the fraction shared by climatic variables and geomorphological history. In the study region, coastal plains are surrounded by a Precambrian basement, the Serra do Mar range, which defines the geomorphology of the region. The Serra do Mar range influences the climate of the region, retaining wet air masses and causing orographic rains and different climates throughout the geomorphological units (Marques et al. 2011). For instance, in southernmost units, coastal plains are more distant from Serra do Mar slope (see Figure 1) and, consequently, show different climates with greater seasonality and lower precipitation (Pers. obs.). Thus, it is reasonable assume that the fraction shared by geomorphological history and climatic variables, could represent a synergic influence of these predictors to drive spatial structure of beta diversity. It would be expected since the well-known influence of climatic variables shaping the distribution range of species, owing to their relationship with species grinellian niche (see Soberón 2007), and

consequently affecting the structure of ecological communities. For example, temperature seasonality can directly affects anuran diversity patterns constraining the distribution of species with narrow niche breadth to occur in environments with less climatic variability (Gouveia et al. 2013).

Spatial variables structured in broad scales (11%, Figure 2) were another relevant predictor to explain the variance in anuran species composition. It is important to note that this fraction cannot be interpreted unambiguously, because it may reflect the effect of unmeasured environmental variables that are spatially structured, as well as, neutral processes which generate positive spatial autocorrelation in ecological communities (Anderson et al. 2011, Tuomisto and Ruokolainen 2006). However, Diniz-Filho et al. (2012) recently tested the importance of neutral processes through spatial autocorrelation analysis in an anuran metacommunity from Amazonia, and found that the spatial component explained 18.5 % which were clearly congruent with neutral predictions about species abundance under neutral dynamics. It indicates the potential role of neutral processes structuring anuran beta diversity. Moreover, fine scale spatial variables explained significantly 7% of the beta diversity, which can represent fine scale processes, such as species biotic interactions (Laliberté et al. 2009, Legendre et al. 2012).

The most important component related to the variation in anuran species composition was the geomorphological history (36%, Figure 2). Indeed, it indicates that historical processes are more important to the community assembly and beta diversity patterns of the region than contemporary processes, such as climatic conditions. There are some theoretical and empirical reasons to ground this finding. First, current patterns of diversity can be a result of historical processes that occurs in regional scales (Ricklefs 2008). For instance, geomorphological barriers can constrain the dispersal of species among areas (Ricklefs 1987), and considering the

assumption of limited species-specific dispersal ability of anurans (Smith and Green 2005), even barriers relatively smaller could to produce spatial patterns of anuran species distribution and composition among areas, i.e., beta diversity. The coastal plains of the region were shaped during quaternary period through of sediments deposition as a result of repeated oceanic incursions (Suguio and Martin 1978). However, these sediments were deposited above of the older Pre-Cambrian rocks (Suguio and Martin 1978), which defined the geological scenario where coastal plains would be shaped and anuran communities would be established, through colonization from surrounding habitats, such as ombrophilous forests of the Serra do Mar. This geological scenario divides the region through narrow headlands with higher elevations (see Figure 1), creating potential barriers to species dispersal between geomorphological units, evidencing that the complex geomorphological history of the region has played an important role in spatial variation of the species anuran composition.

Moreover, this historical influence in the beta diversity patterns of the region could indicates the effect of other historical processes rather than exclusively potential barriers to dispersal. Beta diversity patterns can be related with diversification patterns of regional biota (Qian et al. 2005). Among hypotheses about diversification patterns in the Atlantic Forest, the most well-known is based on the Pleistocene refugia model (Haffer 1969, Grazziotin et al. 2006). This hypothesis posits that Pleistocene glacial cycles have caused multiple vicariance events in the populations of species not adapted to non-forested habitats, owing to the retraction of suitable forested patches, and creating stable refugia during the dramatic climatic changes in glacial periods (Haffer 1969, Grazziotin et al. 2006). An alternative hypothesis emphasizes older processes like orogeny in the late Tertiary, characterized by uplifting of the east coast of Brazil which caused geographic and climatic modifications (Grazziotin et al. 2006).

Phylogeographic studies have shown mixed species-specific results, corroborating these two hypotheses about diversification in the Atlantic Forest (e.g., Grazziotin et al. 2006, Carnaval et al. 2009, Fitzpatrick et al. 2009, Amaro et al. 2012). However, such studies has revealed a clear spatial pattern of divergence which divides lineages of the southern and northern regions from São Paulo state (Grazziotin et al. 2006, Fitzpatrick et al. 2009, Amaro et al. 2012, Bell et al. 2012). This patterns occurs, either due to potential existence of distinct refugia in the northern and southern regions (Fitzpatrick et al. 2009), or by recent southern colonization by populations from northern, during Pleistocene (Carnaval et al. 2009), or even by phylogeographic breaks associated with older tectonic activity (Amaro et al. 2012). Moreover, lowland-restricted species are presumably unable to tolerate cold temperatures of montane regions, and then were more susceptible to the dramatic climatic oscillations of Pleistocene (see Amaro et al. 2012). Therefore, it is plausible that such events, which created patterns of divergence between lineages, also have influenced patterns of species distributions and consequently generate a spatial signature in the beta diversity patterns along coastal plains of the study region.

As correlative approaches do not imply causation by processes, attention is necessary to interpret fractions of explained variation (Anderson et al. 2011). Additionally, recent criticisms have pointed out statistical limitations of variation partitioning approach to estimate accurately the relative contributions of predictors (e.g., Gilbert and Bennett 2010). However, this approach still provides useful tools as a first step to disentangling important processes related to beta diversity patterns (Dray et al. 2012, Heino et al. 2012), as showed here. Our results evidenced a clear influence of the historical processes shaping the spatial structure of anuran beta diversity from the coastal plains of the region. This historical influence can shed light to the understanding about processes which originate and maintain biodiversity in a community level in the Atlantic

Rain Forest hotspot. Nonetheless, our study also highlighted the importance of consider explicitly variables that represent historical processes, associated with contemporary variables, in order to evidence the synergic effects of distinct sets of predictors to beta diversity, as such effects are inherent from the complex nature of ecological communities.

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Table 1 Correlation between climatic variables and PCA axes.

Climatic Variables	PCA axis 1	PCA axis 2	PCA axis 3
Temperature seasonality	0.90	0.30	0.06
Mean temperature of coldest month	-0.69	-0.69	0.003
Precipitation seasonality	0.80	-0.51	0.26
Precipitation of the driest quarter	-0.87	0.38	0.31

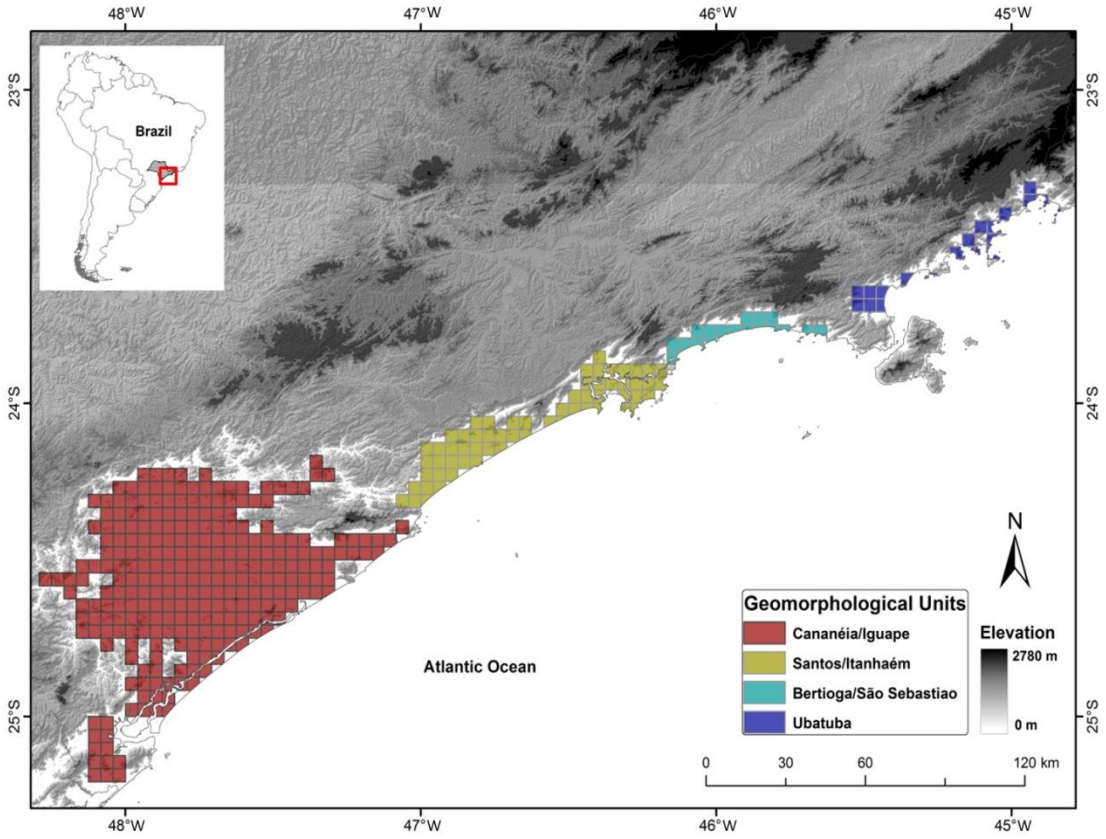


Figure 1. Map of the study region showing grid cells grouped by geomorphological units described by Suguio and Martin (1978) (see text).

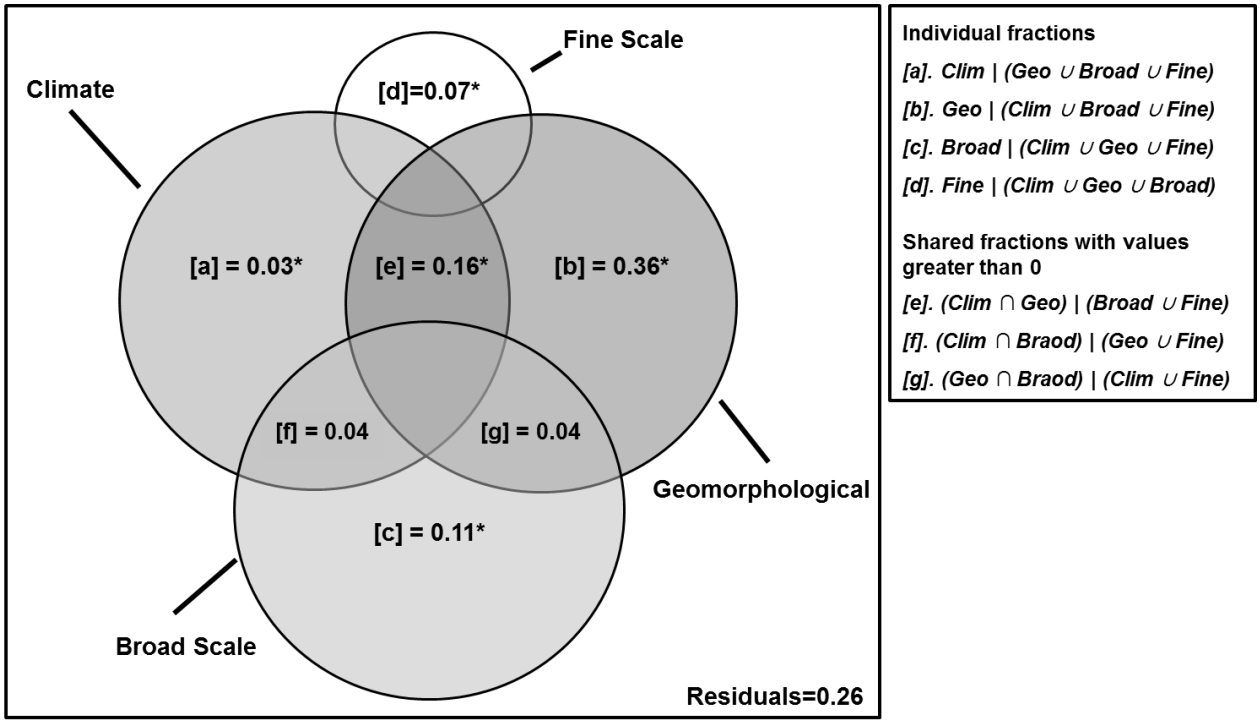


Figure 2. Diagram representing variation partitioning analysis and showing fractions of explained variance. Explained variance of the beta diversity was partitioned in shared and unique fractions of climatic (**Clim**), geomorphological (**Geo**), broad (**Broad**), and fine (**Fine**) scale predictors. Fractions [a], [b], [c], and [d] represent the unique effects of the **Clim**, **Geo**, **Broad** and **Fine**, respectively. Fractions [e] to [g] represent intersections, that is, joint effects of different predictors after controlling for effects of remain predictors (i.e., "covariables" in RDA model). Residuals are the fraction not explained by any predictors included in the model. The upright and downright boxes represent the notations to each set (i.e., fraction). The symbol "∩" represent intersection, "∪" represent union, and " | " represent after controlling for. Fractions with values lower than 0 are not showed in the diagram. (*) means significant fractions tested with permutations tests.

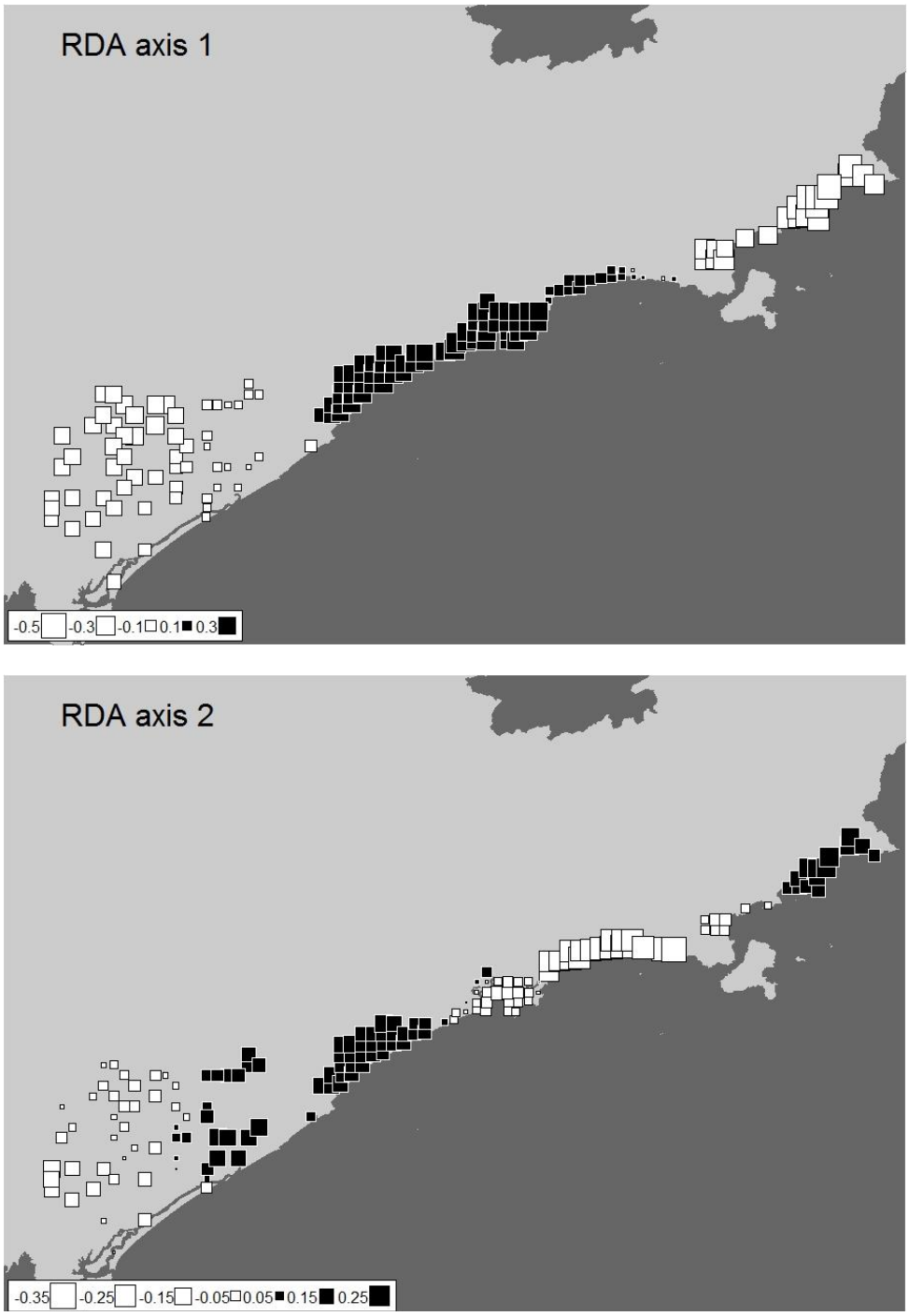
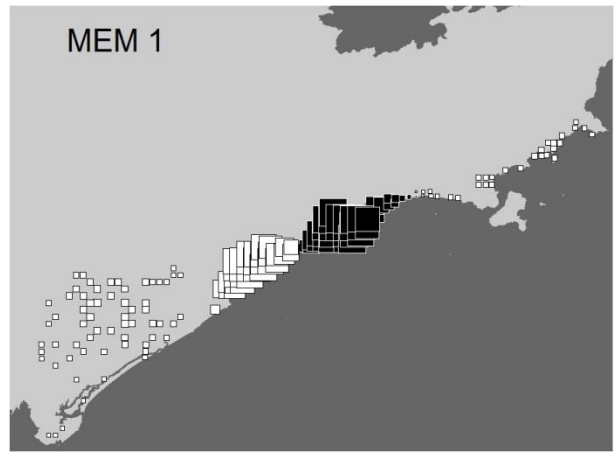
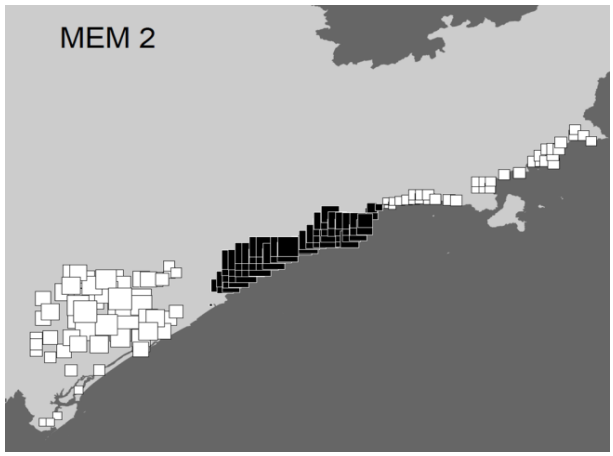
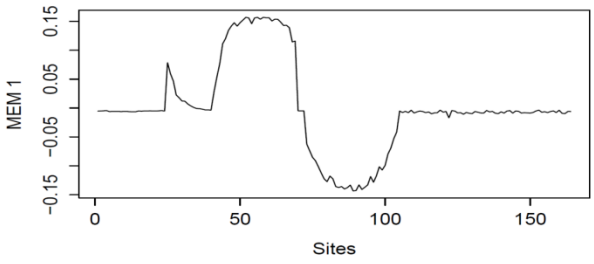
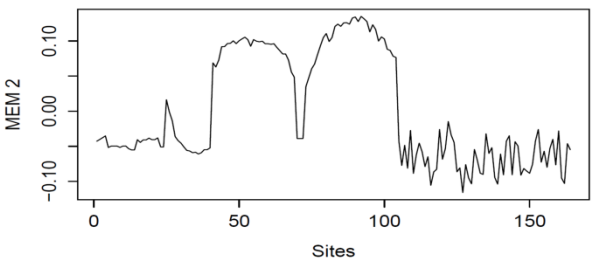


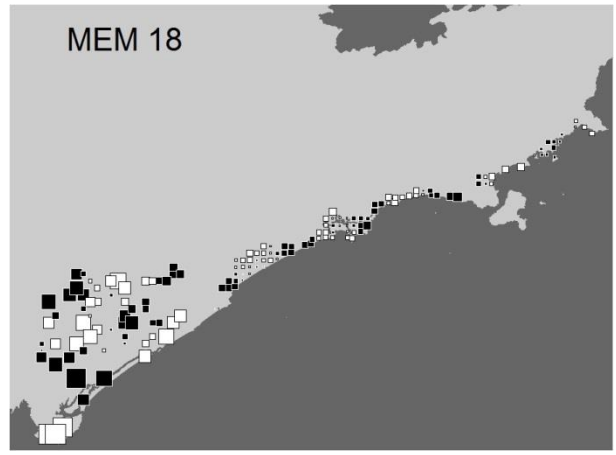
Figure 3. Maps represent of the site scores from the two first RDA axes of the anuran beta diversity constrained by all predictors (i.e., geomorphological, climatic, broad, and fine scale variables), which described 58% of the variation in the anuran composition of the studied region.

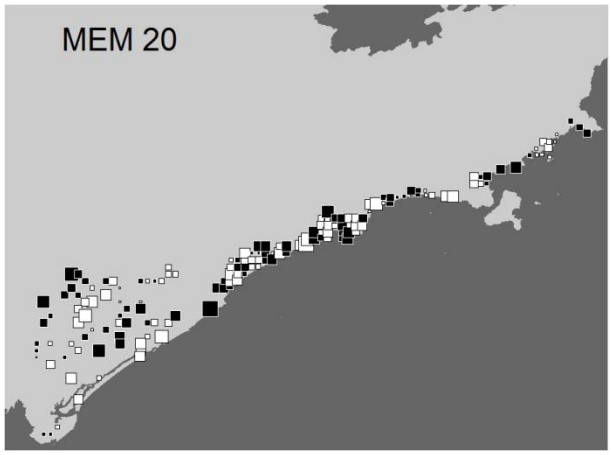

MEM 1

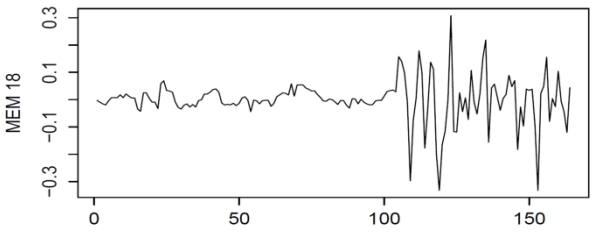

MEM 2


MEM 1
0.15
0.05
−0.05
−0.15
0
50
100
150
Sites


MEM 2
0.10
0.00
−0.10
0
50
100
150
Sites


MEM 18


MEM 20


MEM 18
0.3
0.1
−0.1
−0.3
0
50
100
150

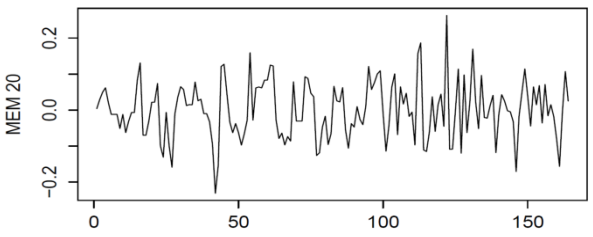

MEM 20
0.2
0.0
−0.2
0
50
100
150

Figure S1. Examples of the Moran Eigenvector Maps (MEMs) classified as broad (i.e., MEM 1 and 2) and fine scales (i.e., MEM 18 and 20). Squares in the maps represent scores of each site in the MEMs. White squares have negative scores and black squares have positive scores. Squares size are proportional to score value. These values are also represented in the graphs below of the maps, which able us to identify similarity in the periods ("modulation") between MEMs.

CONSIDERAÇÕES FINAIS

- A região apresentou 57 espécies de anuros, pertencentes a 22 gêneros e 10 famílias. A riqueza média por célula de 2.5 arc minutos (cerca de 5 km²) foi de 36 espécies, com amplitude de 29 a 44 e desvio padrão 4 espécies.
- Existe uma clara estrutura espacial na diversidade beta de anuros nas planícies costeiras no sudeste do Brasil, que evidencia mudanças na composição de espécies congruentes com a estrutura geomorfológica da região.
- A substituição de espécies contribui mais para a diversidade beta, em relação ao aninhamento, o que também foi observado nas áreas protegidas.
- Apenas 11.3% da área de estudo é atualmente protegida sob a forma de unidades de conservação.
- A diversidade beta da região está estruturada espacialmente em ampla escala.
- O preditor mais importante para explicar a diversidade beta é a história geomorfológica da região, caracterizada a partir de suas planícies costeiras quaternárias que são separadas por pontões de rochas pré-cambrianas da Serra do Mar.
- A fração compartilhada entre preditores climáticos e história geomorfológica foi a segunda fração mais importante, evidenciando a influência de efeitos sinérgicos na estrutura espacial da diversidade beta devido a interação desses dois preditores.
- Preditores espaciais de larga escala são o terceiro conjunto de preditores que melhor explicam a variação na composição de anuros.